A

MANUAL OF BOTANY

ANATOMICAL AND PHYSIOLOGICAL

FOR THE USE OF STUDENTS

BY

ROBERT BROWN

M.A. Ph.Dr. F.L.S. F.R.G.S.

Honorary Secretary, and formerly President, of the Royal Physical Society;
Vice-President of the Botanical Society of Edinburgh; Commander and Government Agent of the Vancouver Exploring Expedition; Botanist of the British Columbia Expedition; Botanist of the '67 Greenland Expedition, &c. &c.

LECTURER ON BOTANY, EDINBURGH

WILLIAM BLACKWOOD AND SONS
EDINBURGH AND LONDON
MDCCCLXXIV

PRINTED BY WILLIAM BLACKWOOD AND SONS, EDINBURGH.

TO

JOSEPH DALTON HOOKER,

C.B. M.D. LL.D. D.C.L. V.P.L.S.

DIRECTOR OF THE ROYAL GARDENS, KEW;
PRESIDENT OF THE ROYAL SOCIETY OF LONDON;
ETC. ETC.

◆

DEAR DR HOOKER,

I know that the age of Dedications—when Dedications simply meant fulsome flattery—is gone by. But I trust that the respectful gratitude which a pupil owes to a master, and to one whose bright example and kindly words have stimulated him under many discouragements—and it may be with little success and much faint-heartedness—to tread the same path in life, never grows old. May I therefore be permitted to embrace the opportunity which the publication of the very modest task embraced in these pages presents, to express my sense of the value of your labours in the cause of botanical science, and of the many kindnesses you have ever shown me. "Sic redit ad dominum, quod fuit ante suum."

With great respect, allow me to remain,

DEAR DR HOOKER,

Your faithful friend,

ROB. BROWN.

PREFACE.

If any apology is necessary for adding one more to the already existing text-books of Botany, it would be found in the ever-changing state of the science, in the new aspects it has assumed by the discoveries of the last few years, and by the ever-accumulating pile of materials which the industry of the busy workers in the French and German laboratories—for vegetable physiology is almost dead in Britain—are continually pouring forth. The task I have laid out for myself in this Manual has been to digest, for the use of the student, this mass of material as perfectly as the natural difficulties and intricacy of the subject will admit of; to present in one view, within a moderate compass, an outline of the chief facts and researches scattered through hundreds of memoirs, *brochures*, volumes, transactions of learned societies, and journals in nearly every European language; and, without overlaying the line of argument and reasoning, where such exists, with too great a multiplicity of facts and examples, to present, in a form fit to be assimilated by the really earnest worker, a comprehensive view of the anatomy and physiology of flowering plants, as elucidated by the best teachers of our day.

Whether I have succeeded in this laborious though unpretentious task, it is not for me to say. I can only hope that I have; for in order to do so, no labour has been spared. Upwards of twelve hundred separate papers and treatises, in German, French, English, and to a less extent in Danish, Swedish, Dutch, Spanish, and Italian, have been consulted

—often without a greater reward than to obtain a single fact, which the exigencies of space have compelled to be relegated to a footnote or a parenthesis. To mention every datum discovered by the hundreds of workers in our science during the last forty or fifty years, even had this been advisable, would have been impossible. I trust, however, that few facts of importance have been omitted, or the more important labours of any of my *confrères* passed over. To have thus unintentionally done injustice to any one would be a sincere cause of regret to me. So rapid is, however, the advance of the science, that while these pages were passing through the press, interesting observations were being published which might have found a place in the body of the book under their proper headings. Such, for instance, not to enumerate foreign researches, are the observations of Professors M'Nab and Thisleton-Dyer on the Perigynium or Utricle of the genus *Carex* (Journ. Linn. Soc. Bot., xiv. 152, 154)—clearly proving from its development that it cannot be looked upon as perianthal or staminal (as Bentham[1] believed), but as bracteal, or "equivalent to the sheath of the foliage leaf;" and the additional observations of Professor Dickie on the buds of *Malaxis* in the same journal (p. 180), confirming his former results, which I have noted in this text-book (p. 369).

Every text-book must necessarily be more or less a compilation; for the science of Botany has been built up by the combined labours of many workers, whose researches it ought to be a digest of. To make it anything else would be simply to convert an impartial *résumé* of the state of the science into a one-sided view of the author's crotchets, regarding the value and truth of which he is the worst possible judge. I may, however, be allowed to mention, that in many cases I have delayed giving an account of any observations which seemed improbable, until by personal examination I had satisfied myself of their truth or erroneousness. This course, while in various cases helping to weed the pages of some useless matter, bulks little from any other point of view, and has delayed the

---

[1] Nature, March 13, 1873.

publication of the book considerably. In the plan of it, I have followed what experience has told most teachers to be the best way of introducing a student to the science, though I have avoided what in some eyes may be looked upon as a fault—the elaborate account of the development of plants, as usually given in German text-books. To have done so would have taken up much space both in text and woodcuts, without a corresponding advantage; for without going over the work himself, it would have been impossible for the student to have followed it. I have, however, given the *result* of these observations, which is the main thing. In a text-book, it is not only necessary to give the newest researches—for the newest and the truest are not always synonymous—but to give the views generally taught and believed in. This repeated visits to all the chief botanical schools of Europe and America have enabled me to do.

Illustrations are supplied wherever absolutely necessary. Too many illustrations often not only confuse the student, take up space where it might be better employed, but take him from nature itself. Ten minutes' examination of the most common plant will teach more than an atlas of the best figures ever can. Those inserted here are, by arrangement with the publishers, chiefly from the excellent 'Eléments de Botanique' of M. le Professeur Duchartre, drawn by the Chevalier Riocreux, and M. Germain de St Pierre's 'Nouveau Dictionnaire de Botanique,' to both of which works I have necessarily been much indebted. Others are supplied from the various sources noted. Some are original; and for a few I am indebted to the accomplished pencil of Mr Roger Hennedy, Lecturer on Botany in the Andersonian University, Glasgow.

As half the student's education is to know familiarly the names of the workers in his science, and to be enabled to extend his knowledge by perusal of memoirs treating of special subjects more fully than the limited space of a text-book can, I have given a bibliography of each subject as fully as necessary. In every case I have scrupulously endeavoured to verify the references; and where I have not been able to do this, the authorities are given for them. If accidentally I have omitted to give my authority for any fact, I must beforehand apologise to the unknown author, and plead that, as the book was originally to a great extent prepared as lectures for my own students, I might have neglected at the time to note the exact reference, and when too late was unable to do so.

In two respects I have departed from the time-honoured conventionality prevailing in text-books. The science has got now so extensive, that if the student is to get in a "manual" of this nature anything better than a merc smattering of the well-worn facts of the science, so interlarded, as to be most repulsive, with technical names—in use, obsolete, or which ought to be abolished, or rather never to have seen the light of print—it is impossible to cram into one moderately-sized volume anatomy, physiology, classification of the natural orders, palæo-phytology, and phyto-geography. Either the volume must become inconveniently bulky, or the outline given be so meagre as to be next to useless. I have therefore adopted the method now very generally coming into use both in lectures and text-books—viz., to divide the two departments of the science. Accordingly, in this volume only the anatomy and physiology of flowering plants are treated of. In another, the history of the science, the description of the natural orders, with the economic and medicinal plants, the extinct species, the method of studying the science, and the laws regulating the distribution of plants over the world, according to the latest views, will be given. Both volumes, though complementary to each other, will be entirely separate treatises, each complete in itself. The description of the physiology of the cryptogamia or flowerless plants I have not mixed up with that of the flowering ones. My own experience as a student and teacher of Botany, now extending to upwards of twenty years, as well as that of others with an infinitely wider knowledge of the requirements of the young botanist, has taught me that to do otherwise only embarrasses and confuses the student. The modes of reproduction in the lower orders of plants are so intricate and varied that they are better studied each under the head of the natural order to which it belongs. Accordingly, in the 'Manual of Botany, Systematic and Geographical,' the anatomy and physiology of the cryptogamia will be fully described.

Microscopists are now so generally adopting the millimetre as the standard of measurement, that whenever I have occasion to notice observations in which the measurements are in this unit, I have not reduced them to the English standard. To enable the student imperfectly acquainted with the convenient decimal standard to do so, there is appended a table (p. xii.) of English and French lineal measures, as well as one showing the different thermometrical scales. The Index and Glossary will contain an explanation of almost every word in use not explained in the body of the book. Those who desire a fuller vocabulary will find it in the late Professor Henslow or Mr Cooke's excellent dictionaries of botanical terms (to both of which I have been often indebted), or in M. Plee's 'Glossologie Botanique.' Coiners of botanical terms seem, however, too often to have forgotten that the names are for the science, not the science for the names. Every assistance rendered me I have carefully acknowledged; but in writing the chapter on "The Ultimate Constituents of the Plant," my gratitude is especially due to Professor Johnson of Yale's works, and to my friend Mr J. Falconer-King, City Analyst of Edinburgh, for timely hints and assistance. Lastly, though in drawing up this *résumé* of vegetable anatomy and physiology the writer has experienced what all compilers of such books must ever do—the accumulation of material beyond the power to make use of it—he trusts that throughout he has ever remembered John Dryden's advice,—"not to write all he can, but all he ought."

R. BR., *Campst.**

BOTANICAL LABORATORY, SCHOOL OF ARTS,
EDINBURGH, *May* 1874.

---

* At the suggestion of M. Alphonse de Candolle, I have adopted the affix *Campsterianus*, to distinguish me—a not very difficult matter—from the late illustrious botanist of the same name.

TABLE I.—FOR CONVERTING MILLIMETERS INTO ENGLISH INCHES AND DECIMALS.

A millimetre equals 0.03937079 *English inch.*

Milli-metres.	Inches.	Milli-metres.	Inches.	Milli-metres.	Inches.	Milli-metres.	Inches.	Milli-metres.	Inches.
661	26.024	687	27.048	713	28.071	739	29.095	765	30.119
662	26.063	688	27.087	714	28.111	740	29.134	766	30.158
663	26.103	689	27.126	715	28.150	741	29.174	767	30.197
664	26.142	690	27.166	716	28.189	742	29.213	768	30.237
665	26.182	691	27.205	717	28.229	743	29.252	769	30.276
666	26.221	692	27.245	718	28.268	744	29.292	770	30.316
667	26.260	693	27.284	719	28.308	745	29.331	771	30.355
668	26.300	694	27.323	720	28.347	746	29.371	772	30.394
669	26.339	695	27.363	721	28.386	747	29.410	773	30.434
670	26.378	696	27.402	722	28.426	748	29.449	774	30 473
671	26.418	697	27.441	723	28.465	749	29.489	775	30.512
672	26.457	869	27.481	724	28.504	750	29.528	776	30.552
673	26.497	699	27.520	725	28.544	751	29.567	777	30.591
674	26.536	700	27.560	726	28.583	752	29.607	778	30.630
675	26.575	701	27.599	727	28.623	753	29.646	779	30.670
676	26.615	702	27.638	728	28.662	754	29.686	780	30.709
677	26.654	703	27.678	729	28.701	755	29.725	781	30.749
678	26.693	704	27.717	730	28.741	756	29.764	782	30.788
679	26.733	705	27.756	731	28.780	757	29.804	783	30.827
680	26.772	706	27.796	732	28.819	758	29.843	784	30.867
681	26.812	707	27.835	733	28.859	759	29.882	785	30.906
682	26.851	708	27.875	734	28.898	760	29.922	786	30.945
683	26.890	709	27.914	735	28.938	761	29.961	787	30.985
684	26.930	710	27.953	736	28.977	762	30.001	788	31.024
685	26.969	711	27.993	737	29.016	763	30.040	789	31.064
686	27.008	712	28.032	738	29.056	764	30.079	790	31.103

Tenths of a Millimetre in the Decimal of an Inch.

0	1	2	3	4	5	6	7	8	9
0.000	0.004	0.008	0.012	0.016	0.020	0.024	0.028	0.031	0.035

TABLE II.—COMPARISON OF THE CENTIGRADE THERMOMETER WITH FAHRENHEIT'S AND REAUMUR'S, GIVING THE CORRESPONDING VALUES FOR EACH DEGREE, FROM +50° TO —41° CENTIGRADE.

Cent.	Fahr.	Reau.	Cent.	Fahr.	Reau.	Cent.	Fahr.	Reau.	Cent.	Fahr.	Reau.
°	°	°	°	°	°	°	°	°	°	°	°
50	122.0	40.0	27	80.6	21.6	4	39.2	3.2	—19	— 2.2	—15.2
49	120.2	39.2	26	78.8	20.8	3	37.4	2.4	—20	— 4.0	—16.0
48	118.4	38.4	25	77.0	20.0	2	35.6	1.6	—21	— 5.8	—16.8
47	116.6	37.6	24	75.2	19.2	1	33.8	0.8	—22	— 7.6	—17.6
46	114.8	36.8	23	73.4	18.4	0	32.0	0.0	—23	— 9.4	—18.4
45	113.0	36.0	22	71.6	17.6	— 1	30.2	— 0.8	—24	—11.2	—19.2
44	111.2	35.2	21	69.8	16.8	— 2	28.4	— 1.6	—25	—13.0	—20.0
43	109.4	34.4	20	68.0	16.0	— 3	26.6	— 2.4	—26	—14.8	—20.8
42	107.6	33.6	19	66.2	15.2	— 4	24.8	— 3.2	—27	—16.6	—21.6
41	105.8	32.8	18	64.4	14.4	— 5	23.0	— 4.0	—28	—18.4	—22.4
40	104.0	32.0	17	62.6	13.6	— 6	21.2	— 4.8	—29	—20.2	—23.2
39	102.2	31.2	16	60.8	12.8	— 7	19.4	— 5.6	—30	—22.0	—24.0
38	100.4	30.4	15	59.0	12.0	— 8	17.6	— 6.4	—31	—23.8	—24.8
37	98.6	29.6	14	57.2	11.2	— 9	15.8	— 7.2	—32	—25.6	—25.6
36	96.8	28.8	13	55.4	10.4	—10	14.0	— 8.0	—33	—27.4	—26.4
35	95.0	28.0	12	53.6	9.6	—11	12.2	— 8.8	—34	—29.2	—27.2
34	93.2	27.2	11	51.8	8.8	—12	10.4	— 9.6	—35	—31.0	—28.0
33	91.4	26.4	10	50.0	8.0	—13	8.6	—10.4	—36	—32.8	—28.8
32	89.6	25.6	9	48.2	7.2	—14	6.8	—11.2	—37	—34.6	—29.6
31	87.8	24.8	8	46.4	6.4	—15	5.0	—12.0	—38	—36.4	—30.4
30	86.0	24.0	7	44.6	5.6	—16	3.2	—12.8	—39	—38.2	—31.2
29	84.2	23.2	6	42.8	4.8	—17	1.4	—13.6	—40	—40.0	—32.0
28	82.4	22.4	5	41.0	4.0	—18	—0.4	—14.4	—41	—41.8	—32.8

Comparison of the Scales for each Tenth of a Degree.

Cent. . . .	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
Fahr. . . .	0.18	0.36	0.54	0.72	0.9	1.08	1.26	1.44	1.62	1.8
Reau. . . .	0.08	0.16	0.24	0.32	0.4	0.48	0.56	0.64	0.72	0.8
Fahr. . . .	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
Cent. . . .	0.06	0.11	0.17	0.22	0.28	0.33	0.39	0.44	0.5	0.56
Reau. . . .	0.04	0.09	0.13	0.18	0.22	0.27	0.31	0.36	0.4	0.44
Reau. . . .	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
Fahr. . . .	0.22	0.45	0.67	0.9	1.12	1.35	1.57	1.80	2.02	2.25
Cent. . . .	0.12	0.25	0.37	0.5	0.62	0.75	0.87	1.00	1.12	1.25

CONTENTS.

INTRODUCTION.

SECTION I.—General Anatomy or Histology of the Elementary Tissues.

CHAPTER I.

CELLULAR TISSUE OR PARENCHYMA.

CHAPTER II.

WOODY AND VASCULAR TISSUES.

CHAPTER III.

EPIDERMIS AND APPENDAGES.

SECTION II.—Nutrition.

CHAPTER I.

THE STEM.

CHAPTER II.

THE ROOT.

CHAPTER III.

THE LEAF.

CHAPTER IV.

THE ULTIMATE CONSTITUENTS OF PLANTS.

CHAPTER V.

THE FUNCTION OF NUTRITION.

SECTION III.—Reproduction.

CHAPTER I.

GENERAL REMARKS ON THE FLOWER AND FLOWERING.

CHAPTER II.

THE PERIANTH, OR FLORAL ENVELOPES.

CHAPTER III.

THE ANDRŒCIUM, OR STAMINAL WHORL.

CHAPTER IV.

THE GYNŒCIUM, OR PISTILLINE WHORL.

CHAPTER V.

DEVELOPMENT, PRÆFLORATION, SYMMETRY, AND METAMAPHOSIS.

CHAPTER VI.

DISC AND NECTARIES.

CHAPTER VII.

INFLORESCENCE OR ANTHOTAXIS.

CHAPTER VIII.

FERTILISATION OF THE OVULE: ORTHOGAMY.

CHAPTER IX.

FERTILISATION: HETEROGAMY.

CHAPTER X.

THE FRUIT.

CHAPTER XI.

THE SEED.

CHAPTER XII.

GERMINATION.

CHAPTER XIII.

GRAFTING : LONGEVITY OF PLANTS, ETC.

SECTION IV.—General Phenomena connected with Plant-life.

CHAPTER I.

HOMOPLASMY : MOVEMENTS AND SPECIAL DIRECTIONS IN PLANTS.

CHAPTER II.

OPENING AND CLOSING OF FLOWERS: SLEEP OF PLANTS.

CHAPTER III.

VEGETABLE IRRITABILITY, AND MOVEMENTS OF CLIMBING PLANTS.

CHAPTER IV.

ODOURS, COLOURS, LUMINOSITY, TEMPERATURE, AND NOSOLOGY OF PLANTS.

ERRATA.

Page 49, line 45, *for* "Tyloses" *read* "Tylosis," *and add reference*, "Thiselton-Dyer, Journ. of Bot., Nov. 1872; Caird, Trans. Bot. Soc. Edin., xi. 496."
Page 128, line 16, *for* "petiole forming" *read* "result being."
,, 164, ,, 18, *for* "Leniceraceæ" *read* "Loniceraceæ."
,, 218, ,, 40, 44, *for* "Aleurine" *read* "Aleurone."
,, 288, ,, 46, *for* "Periclenium" *read* "Periclinium."
,, 407, ,, 43, *for* "ετερος, crooked," *read* "Ἕτερος," other.
,, 494, ,, 25, *for* "Glabulus" *read* "Galbulus."
,, 398, ,, 9, *delete* "And the so-called panicle."
,, 468, fig. 311, *for* "Anassa" *read* "Ananassa."
,, 491, line 6, *for* "Sphacerocarpium" *read* "Sphalerocarpium."

MANUAL OF BOTANY.

INTRODUCTION.

BOTANY,[1] or *Phytology*,[2] is that department of biological science which treats of the nature, functions, and classification of plants, and of the relation of these plants one to another, to the animal kingdom, and to the forces of inanimate nature—in a word, it is to the vegetable kingdom what Zoology is to the animal—the history, in the broadest sense, of the beings composing it.

If the relative importance of the subject of which any science treats is to be taken as a criterion of the interest or importance of that science, then the one to an exposition of which the following pages are to be devoted ranks high in the list. Without plants the earth would be a dreary uninhabitable desert throughout a vast portion of its extent, and man reduced to a condition somewhat similar to that of the Eskimo—tribes of miserable fishers and maritime hunters. It is even questionable if he could exist; for many of the marine animals, and all of the terrestrial ones, are indirectly or directly dependent for their subsistence on the vegetable kingdom. Plants furnish the food of herbivorous animals, and the animals in their turn give nourishment to vast tribes of other beings called carnivorous—including man himself. The vegetable kingdom also furnishes a great portion of the food of the human family, as well as its clothing, medicine, fuel, and the material for its dwellings, and implements of domestic economy, of the arts and manufactures, of war and peace. The earth owes her beauty to the flowers and green leaves of plants; and the very air we breathe, the water we drink, and the food which nourishes us, are alike dependent on the vegetable kingdom. The plant could do without man, as in ages past it did—the flower could bloom in the lonely desert or umbrageous forest, as it still does over regions of the

---

[1] Βοτάνη, a plant.

[2] Φυτόν, a plant; λογός, a discourse.

earth undisturbed by the human race; but man could not subsist, except in the lowest condition of savagedom, without its aid. Independently, however, of the mere economic importance of plants, they afford an insight into many interesting and complicated phenomena of nature, both past and present, and present a field for study so extensive, that Botany might in any of its various departments furnish a field wide enough for the industry of a lifetime.

At the very outset of our study we are met by the question, What distinguishes plants from animals? When we look at the oak and the elephant, the question might seem an idle one; and it is only when we approach the confines of the two animated kingdoms that we see how difficult it is to draw a line between the lower members of each, or to say where the plant ends and the animal begins, though between the mineral and the animated kingdoms there is a hard and fast line of demarcation—viz., the possession of the vital principle, in addition to many others subordinate to and dependent on this. Chief among these are the powers of *nutrition* or self-support, by which all organised beings can *assimilate* within their constitution the particles of other bodies, by which each individual member increases in size, and so *grows* and maintains life; and secondly, the power of *reproduction*, by which each individual member can produce others resembling itself, and so increase and perpetuate its kind. Unorganised substances can do neither.

Such being the ground common to plants and animals, we next come to consider what is the *distinction* between them; and here we are at fault. Motion, we shall find, is a characteristic not peculiar to the animal kingdom, but is found throughout life in some of the lower members of the vegetable kingdom; and equally we shall have occasion to discuss, in the course of our study, a certain irritability, and even instinct, which it is almost impossible, without drawing an arbitrary distinction, to characterise as very different from that found in some of the lower animals. Even in composition some animals do not differ from plants; the presence of the substance called "cellulose" (p. 17) —once supposed to be a constant element found in the latter only—having been discovered to a large extent in some of the ascidian molluscs, and even in the low forms of animal life called *coccospheres*. The difficulty of drawing a distinction between plants and animals is, however, one more of words than reality; for, as we have said, it is only when we approach the shadowy boundaries of the two kingdoms that we find any difficulty in seeing the respective lines which divide the regions of the botanist and zoologist. The following characteristics may therefore, in the present state of our knowledge, be accepted as true: (1.) Plants alone can subsist directly on the mineral kingdom, and on the surrounding air and moisture, and assimilate these elements into organised structure. (2.) The permanent fabric of plants is composed of *ternary* compounds—*i. e.*, substances composed of three elements, these being carbon, hydrogen, and oxygen. The tissues of animals contain, in addition, nitrogen, and so are composed of *quaternary* compounds. Contrary to what is commonly stated in some works, the student ought to bear in mind that it is only in the proportion which these elements bear to each other that the members of one kingdom differ from the other, both containing nitrogenous and non-nitrogenous elements, though in those substances in plants (legumen and gluten) which contain nitrogen, it is found in comparatively small quantities. Cellulose, again, with the exception named, is only found in plants; and though chlorophyll, or the green colouring substance of plants (p. 23), has been discovered in some members of the animal kingdom (*e.g.*, *Stentor*, the trumpet animalcule, and *Hydra*, the fresh-water polype), its presence is, as a rule, strong presumptive evidence of the vegetable nature of the organism. (3.) Plants, as a rule, decompose carbonic acid and exhale oxygen—an exception being found in some of the fungi. Some of the last-named plants also require the aid of organised matter for their support.

It necessarily follows that a science so extensive, and taking cognisance of so many points of study, must be divided into subordinate departments for the more convenient acquisition of knowledge, and for the classification of the knowledge so obtained. Looking at any common flowering plant, we see that it is composed of root, leaf, flower, and so on, but these compound organs are in their turn composed of substances which cannot be examined by the naked eye. Hence this leads us at an early stage of our studies to examine the *General Anatomy* or *Histology*[1] of plants. Having proceeded thus far, we next come to consider the different organs made up of these minute ones common to all —viz., the cells and vessels, and their structure and arrangement in reference to one another; this constitutes *Organography*.[2] Furthermore, we shall find, if we examine the relations and developments of the organs of the plant, that these organs are not each formed on a distinct plan, but are only modifications of one type, that type being the leaf; we shall see that the leaves are arranged in whorls along the stem, and that even the component parts of the flower, though generally close together, alternate with one another, and are only modifications of the leaf—this modification being gradual, from the typical leaf to the bracts, sepals, petals, stamens, and pistil. This constitutes the philosophical or

---

[1] ῾Ιστος, a web; λογός, a discourse.

[2] ῎Οργανον, organ; γράφω, I write.

transcendental view of organography, or *Morphology*,[1] and is to botany what comparative anatomy is to Zoology and Zootomy. The special study of the developments of organs has been called *Organogenesis*,[2] completing, as it does with organography, *Phytotomy*,[3] or *Vegetable Anatomy.* All these organs, though modifications of one type, have, however, special and distinct functions to perform—*e.g.*, the root to absorb nutriment, the stem to convey it throughout the plant, the leaves to elaborate it, the flower and its part to form the seed, which in its turn perpetuates the species, the acme of organic existence. The study of this constitutes *Physiological*[4] *Botany.* If we investigate the composition of the substances composing the plant, and their reactions one with another, we enter on the study of *Vegetable Chemistry.* Like all organisms, these functions of the plant are apt to get into an abnormal state, the result being disease, the study of which constitutes vegetable pathology or *Nosology;*[5] or there may be congenital or other abnormalities in the forms of organs, which enable the anatomist often to get an insight into the plan of structure, by, as it were, a lifting up of nature's veil; the study of these is *Teratology.*[6]

Hitherto we have been only looking at the plant as an abstraction, a typical *phyton*, which possibly may not in all its details exist in nature. Plants, however, as the student need not be told, are found in apparently endless forms, all modifications of the typical phyton or model plant, but seemingly with such wide divergences from it that it would be almost hopeless to work all the forms into this type. However, on studying the multiplicity of species scattered over the earth, we shall find that they may be reduced to about three great types of structure, and that each of these in its turn will be found to embrace a number of secondary classes, the members of which have their forms modified on one plan. Each of these classes, again, contains numerous orders embracing plants different one from another, but yet having a general likeness; while each of these is composed of a greater or less number of genera,[7] the species of each genus having a close likeness, showing that, though now different, they may have originally sprung from the same ancestor, or have been formed on the same plan; lastly, each of these species is the type of an

---

[1] Μορφή, form; λογός, a discourse. Properly speaking, however, the word is only a synonym of *organography*, though used in the sense given. *Homology* would be more correct.

[2] Ὄργανον, organ; *γίνομαι*, to grow.

[3] Φυτόν, a plant; *τομή*, division.

[4] Φύσις, nature; λογός, a discourse—the word having now a much more restricted meaning.

[5] Νόσος, disease.

[6] Τέρας, *τέρατος*, monster.

[7] In this general view we do not overlay it by speaking of the minor subdivisions, which will find a place in the section appropriated to classification.

indefinite number of individuals all similar to one another, and each reproducing offspring identical with the parent and the species, any modifications from the specific type being merely accidental, temporary, or too trivial to cause the form so diverging to be classed as otherwise than a variety of the original species, apt to return again to the normal type. The methods adopted in classifying these various forms, the laws regulating the variation of species, &c., form the subject of *Taxology*,[1] *Taxonomy*,[2] *Classification* or *Systematic Botany*. To express in concise language the various modifications of the organs which give each species its separate character, requires a vocabulary both more profuse and more exact than that of ordinary language; accordingly, numerous words, chiefly either of Latin or Greek origin, have been coined for this purpose—the study and acquisition of which is essential to the botanist who would acquire accurate ideas of species; it forms a subdivision of Taxology under the name of *Terminology*[3] or *Glossology*.[4] The art of describing plants has been called *Phytography*[5] or descriptive botany. Plants are not distributed at random over the world—each region has its own species, and certain laws regulate the distribution of the species which give the peculiar physiognomy to the vegetation of each region; hence we have *Phyto-geography*,[6] or the study of the laws regulating the distribution of plants, and of different plant regions. When we extend our studies to the rocks which compose the crust of the globe, we find that, in early ages of the world's history, forms of plants more or less widely different from those now living clothed the earth—the remains of these plants being imbedded in a fossil state in the rocks, and that such extinct plants had a widely different distribution from those now growing on the surface. The consideration of these extinct species constitutes *Palæo-phytology*,[7] *geological botany*, *vegetable palæontology*,[8] or simply, *fossil botany*. Lastly, we may consider plants from an *economical* or applied point of view, so that the study may be subdivided into *Medical Botany*, the consideration of the species yielding medical plants; *Agricultural Botany*, the study of the species in cultivation in fields; *Horticultural Botany*, the study of these under cultivation in gardens—the best method of preserving them in health, or of increasing their brilliancy of colour, excellence of fruit, or beauty of form; *Industrial Botany*, an examination of plants from the manufacturer's and merchant's points of view—viz., what ones yield fibres, dyes, gums, timber, &c.; and so on, though the

---

[1] Τάξις, arrangement; λογός, discourse.

[2] Τάξις, arrangement; νόμος, law.

[3] *Terminus*, the end.

[4] Γλῶσσα, the tongue.

[5] Φυτόν, a plant; γράφω, I write.

[6] Φυτόν, a plant; γη, the earth.

[7] Παλαιὸς, ancient; φυτόν, a plant.

[8] Παλαιὸς, ancient; οντα, being.

departments mentioned will probably embrace the chief subdivisions of the science. Luckily, however, for the student, he is not at the outset of his botanical studies called upon to examine plants from any of these points of view exclusively. He must first gain an acquaintance with the general elements of plant history; and in so doing, many, if not all, of these departments will get absorbed under other more general heads, which we shall now proceed to discuss in a systematic manner. Unfortunately (or fortunately), not more in a text-book than in nature is it possible to give what has been called a perfectly "natural classification" of the subjects of study. For instance, though it is necessary for the tyro to know the minute structure of plants before he proceeds to the study of the organs which are composed of these minute structures, yet he will not fully understand the first before he has some acquaintance with the second, and so with all the other departments. From time to time, therefore, he will find it advisable to revise his earlier studies in the light of his more recent ones. Laying aside for the present the division of Botanical science sketched in the foregoing paragraphs, let us consider the biography of the plant under the following headings:—

I. HISTOLOGICAL OR GENERAL ANATOMY.—The history of cells, vessels, &c., their origin and multiplication, and other minute organs common to all parts of the plant. II. NUTRITION.—The organs ministering to the nourishment of the plant, their structure and function. III. REPRODUCTION. — The description of the flower and its modifications and development, the structure and development of the fruit and seed, the methods of impregnation necessary to produce the latter, &c. IV. CRYPTOGAMIA, or the structure and functions of flowerless plants, the previous sections relating only to Phanerogamous or flowering plants. V. GENERAL PHENOMENA OF PLANT LIFE.—In this section will be considered the subjects of irritability, temperature, colour, luminosity, &c.—in a word, subjects which cannot, without breaking the thread of argument, be introduced under any of the foregoing headings. VI. TAXONOMY, or classification and the method of studying and describing species. VII. PHYTO-GEOGRAPHY, or botanical geography. VIII. PALÆO-PHYTOLOGY, or fossil botany—a description of the gradual appearance of plants on the earth up to the present day, and their connection with the present flora, either by descent or consanguinity.

SECTION I.

GENERAL ANATOMY OR HISTOLOGY OF THE ELEMENTARY TISSUES.

IN the preceding pages we have glanced at the plant from a general point of view, and have seen that its organs—leaves, stem, root, flower, &c.—are all varied to subserve certain purposes, though composed of materials seemingly much the same. If we go deeper into the examination of the substance composing these organs, we find that the microscope reveals that the plant, no matter how diversified may be its appearance, size, or habits, is composed of the following elementary tissues : 1. *Cells*, or little bladders, with thin transparent walls, very minute and variable in form, being sometimes regular, at other times irregular in shape ; 2. *Short tubes*, attenuated at either end; 3. *Vessels*, cylindrical or angular, and either scattered through the plant singly, or united in bundles. These three in composition get the names of *cellular tissue*, *woody* or ligneous *tissue*, and *vascular tissue*. Again, though seemingly different, they are only modifications of one and the same thing—viz., the *vegetable cell*. From this are formed, by various modifications, all the organs of the plant; the simplest, as well as the most complex, alike owe their structure to the primary cell. This being so, it becomes important, before we proceed one step further in the examination of the structure and functions of the complex organs, to examine more minutely the elementary tissues of which they are built up. These we shall consider under the heads of *cellular*, *woody*, and *vascular* tissues.

CHAPTER I.

CELLULAR TISSUE OR PARENCHYMA.[1]

CELLULAR tissue[2] is the fundamental organisation of the plant. It is composed of little cells, utricles, or bladders, with very thin walls, firmly united together, and appearing to form a continuous mass. The uniting material of the cells appears to be the *intercellular substance*, which, if the cellular tissue is boiled in water or nitric acid, dissolves out and leaves the disunited cells in their proper form.

Form of Cells.—In shape the cells vary very much. Some are polyhedral, commonly dodecahedral, or in the form of prisms with four, five, or six faces. Sometimes in the same tissue the contiguous cells will vary in shape, as is well shown in fig. 1 of cellular tissue from the pith of the vine.

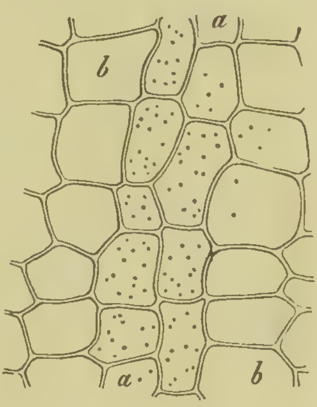


Fig. 1.—Portion of the cellular tissue which forms the pith of the vine, seen in longitudinal section. Here are exhibited cells with six unequal sides, others with five sides, while others have only four. *a a* Dotted cells ; *b b* Cells either unpunctated or very little so.

At first they are almost spherical, especially when they remain isolated. However, in course of time, owing to pressure of the neighbouring cells, multiplication, and other causes, this primitive form becomes much modified. Then they will become more or less angular or polyhedral. In most cases the cell is dodecahedral, so that a section of such a tissue looks at a glance not unlike a section of a honeycomb. The form is, however, rarely perfectly regular, and then only when the cell has been subject to perhaps equal pressure on all sides. More frequently the cells are irregularly hexagonal, one or more of the faces having devel-

---

[1] Παρένχυμα, substance of organs (παρὰ, through ; and ἐνχύω, I infuse).

[2] Also called *Parenchymatous*, areolar, utricular, or vesicular tissue. Hayne (Flora, 1827, ii. 601), Meyen (Phytotomie, 57 ; Physiologie, i. 12), and Morren (Bulletin de l'Acad. de Bruxelles, v. No. 3), have all proposed names for the varieties of this tissue. The nomenclature proposed by Hayne attracted little attention ; while those of Meyen and Morren have been adopted by a few writers,

oped at the expense of the others.[1] So marked is often this irregularity, that it is difficult to reduce the shape to the hexagonal form at all. Under the influence of this pressure, not unrarely we find the cell losing one or other of its sides, and becoming pentagonal or even quadrilateral (fig. 4).

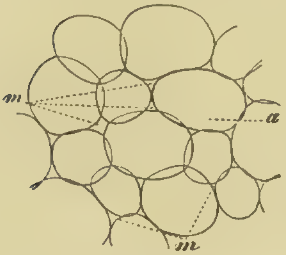


Fig. 2.—Fragment of cellular tissue from the fleshy stem of *Rhipsalis salicornioides*, Haw. *m m* Intercellular passages, almost all triangular, but of which one, much larger, is quandrangular; *a* A cell surrounded by six others.

Lastly, there are the anomalous cells known as *stomata.* Some microscopists, and particularly Charles Morren, have applied particular names to each of these tissues, in accordance with the form of the cells composing it. The chief of these are :—

1. *Rounded Parenchyma*[2] (fig. 2), composed of an aggregation of globular or ellipsoidal cells. It is common in young plants or young organs, and in the soft fleshy parts of plants and fruits.

2. *Polyhedral Parenchyma* (fig. 3).—This is the most common form of cellular tissue—in fact, is that to which the name parenchyma in general refers. The form usually, though not

---

but in most cases of little weight. Both, especially that of Morren, have only served to confuse an already burdensome terminology, and are worthy of the neglect with which they have been treated of late by the best authors. No exact subdivision, such as Morren gave, can be adopted, "because no exact connection exists between the form and function, and frequently enough the same organ is formed of cells differing considerably in form in two closely allied plants." I have given the chief of these names in footnotes, so as to obviate as far as possible the mischief done in some recent books by their injudicious adoption.

[1] No doubt, theoretically, when the cells get collected in masses, as in the pith, &c., each cell being surrounded on all sides by other cells, the form of each individual cell ought to be that of a rhombic dodecahedron, since this form encloses the greatest space within the smallest limits. However, it would be vain to seek for this actually in nature, since the contiguous cells are too unequal in size for them to become moulded into regular mathematical forms by their reciprocal pressure.—Kieser, Grundz. d. Anat. der Pflanzen, § 127; Mohl's Anat. and Phys. of Veg. Cell., Engl. Trans., 6 (an admirable work, which the student should make himself master of, as soon after he has acquired some elementary knowledge as possible. He must, however, remember that much in it has been shown to be erroneous, and that it is to a great extent a defence of many crotchets held by no observer but himself).

[2] *Merenchyma* of Meyer (μηρύω, I revolve), and *Sphærenchyma* (σφαῖρα, a sphere), applied to spheroidal cells, *ovenchyma* (ὠον, an egg), to oval cells, &c., are just modifications of this. These and other terms of a similar nature, applied to modifications of cellular tissue owing to the form of the cells—these modifications often differing very little from each other—are not in general use by the best descriptive writers.

invariably taken, is the hexagonal; hence the various names applied to it.[1]

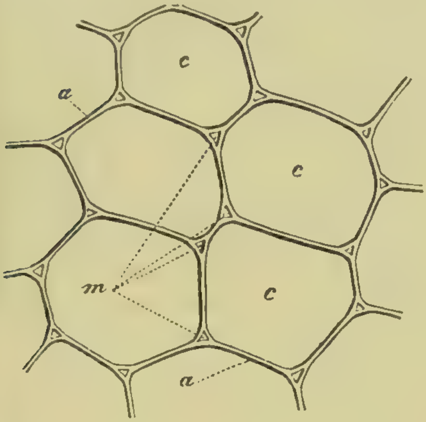


Fig. 3.—Cellular tissue of the bulb of *Lilium superbum*, L. *c c c* Cells viewed on hexagonal section; *m* Intercellular passages appearing triangular; *a* Continuous membrane, which forms the common wall of two adjacent cells.

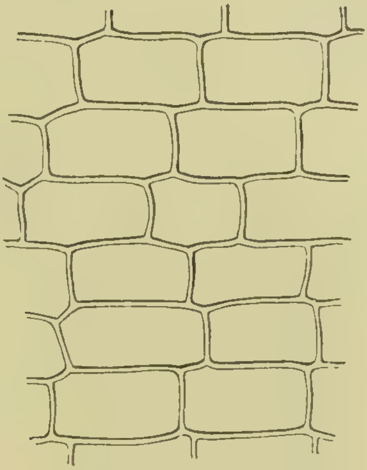


Fig. 4.—Muriform parenchyma, taken from the stem of *Aristolochia Sipho*, L'Hérit. Longitudinal section.

3. *Muriform Parenchyma* (fig. 4).—This tissue is commonly found in the medullary rays of dicotyledonous trees, and derives its name from its cells appearing like bricks in a wall.

4. *Tabular Parenchyma*[2] (fig. 5) is seen in the epidermis of plants, particularly in that of ferns. It derives its name from the fact that it gains in breadth without a corresponding increase in thickness, on account of the pressure of the tissues which it covers; and hence each long thin cell looks like a table without the legs.

In the four different forms of cells which we have noted, there is no thickening of the cell-walls at their junction. In those, the description of which follows, the contrary is the case. Hence the intercellular passages, which will be presently noticed, are increased, and the air has freer access to the surface of the cells. The parenchyma formed by such cells, as would naturally follow, is also always looser and more spongy than that composed of cells more intimately united to each other, as in the four preceding types.

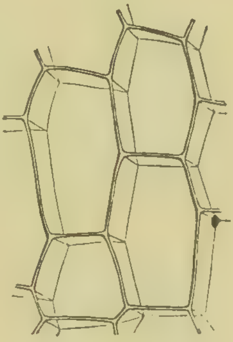


Fig. 5.—Tabular parenchyma from the epidermis of the male fern. (*Aspidium Filix-mas*, Sav.)

---

[1] Hexagonal parenchyma, hexagonal cellular tissue, &c.; or shortly, *hexagonienchyma* (ἑξαγωνιος, six-angled). The *Prismenchyma* (πρίσμα, prism) is only a slight modification of it.

[2] *Pinenchyma* of some authors (πίναξ, a table).

5. *Branched Parenchyma.*[1]—In this case the cells are distinguished by irregular and little marked prominences uniting with the neighbouring cells, and leaving lacunæ between them; hence it is sometimes called *lacunary tissue.* This kind of tissue is commonly found in the layer of parenchyma nearest to the under surface of leaves (fig. 6), or in branched hairs.

6. *Stellate parenchyma.*[2]—When the prominences on the cells assume a more marked character, the cells appear in the form of asterisks, with five or six rays, giving the tissue under the microscope a very characteristic aspect. In this case the intercellular passages are very large. Such a tissue is markedly seen in the stem of aquatic and other plants (*Sagittaria*, *Juncus*, *Musa*, seed-coat of the privet, "white" of the rind of the orange, &c.) In these cases the air gets freer access through the whole interior of the stem, giving plants made up of such tissues a lightness necessary to their mode of existence. In this stellate parenchyma the rays of the cells are unbranched—one or two of the rays being directed downward, the others upwards, to join their neighbours, as in fig. 7.

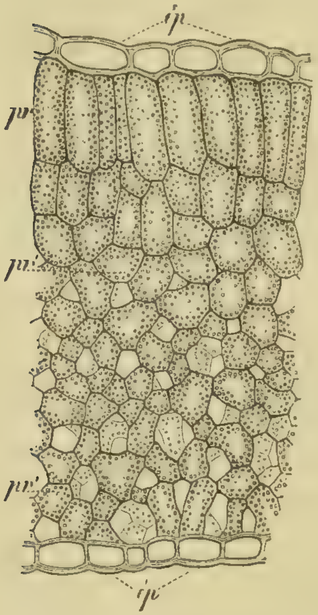


Fig. 6.—Transverse section of a leaf of *Pelargonium inquinans*, Ait., showing branched parenchyma, with lacunæ, *pr' pr'*, of which it is chiefly composed; *pr* "Pallisaded," or upper layer of oblong or ovoid cells; *ép, ép*, Epidermis. The cells are filled with chlorophyll.

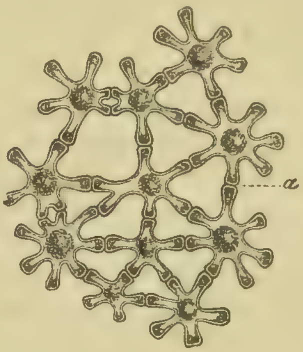


Fig. 7.—Stellate parenchyma, from the stem of *Juncus effusus*, L. *a* Point of union of the extremities of two adjacent cells.

M. Duchartre has very aptly remarked that the organs of plants in the course of their development present in general two successive periods. In the first, the cells, in forming the substance of the plant, multiply without cessation; in the second case, they do not increase, but elongate, following the elongation of the organ in which they are found. In this last-mentioned

---

[1] *Cladenchyma* (κλάδος, a branch).

[2] *Actinenchyma* (ἀκτιν, a ray).

period, the forms of each are notably modified, and the modification operates in different manners, so that we can distinguish two categories of elongated cells.

7. *Elongated cylindrical cells.*—In this case the cells are formed in horizontal lines, which end by forming a cylinder more or less narrow in diameter, and terminating in abrupt or moderately inclined points, as in *Chara.*[1] Caspary, finding these elongated cells in the essential parts of the architecture of plants, and in their interior nitrogenous matter, thinks that they perform an important function in the life of the plant—namely, that they convey the nutritious fluids. Hence he called them *cellulæ conductrices.*[2]

8. *Fusiform cells, fibres or prosenchyma*[3] (fig. 8).—In this kind of elongated cells each terminates in points which insert themselves between the cells of the same kind lying above and below them—in a word, they are spindle-shaped; hence the name (*fuseau,* Fr. a spindle). For the same reason Dutrochet called them *Clostres.*[4] These fusiform cells, when thickened by internal deposits, form the fibrous or resisting portion of wood and bark, and are often called simply *fibres.* It is impossible to give in to the idea of Adrian de Jussieu, and a few other botanists, that prosenchyma is a tissue different altogether from cellular tissue. All transitions from the one to the other can be traced, showing that the fibres commence with cells becoming closed.

Fig. 8.—An isolated fusiform cell of the prosenchyma of *Bragantia tomentosa,* Bl. *pp'* punctations.

The following table, after Duchartre, shows at a glance the characteristics of the eight different tissues which we have been describing. Some authors whose delight is more in nomenclature than real science have distinguished others, but we cannot see that they are marked by any characteristics sufficiently salient to cause us to enlarge our already too extended catalogue by their mention.

---

[1] Sometimes this kind of cellular tissue is called *Cylindrenchyma* (κύλινδρος, a cylinder) by some authors.

[2] *Leitzellen* in German.

[3] Πρός, and ἔνχυμα, strong substance; or *Atractenchyma* (ἄτρακτος, a spindle).

[4] Κλωστὴρ, κλωστῆρος, spindle.

		CELLS.	TISSUES.
SHORT CELLS OR PARENCHYMA.	United exteriorly, or without prominences.	Globular or ovoid cells, showing in section a rounded or oval aspect, .	Rounded parenchyma.
		Polyhedral cells, showing a hexagonal section, ...	Ordinary or polyhedral parenchyma.
		Parallelopiped, showing a rectangular section, ...	Muriform parenchyma.
		Cells in a tabular form, showing at least a rectangular elongated section, ...	Tabular parenchyma.
	With prominences or ramifications.	Branched cells, or with short angular prominences, . . .	Branched or lacunary parenchyma.
		Rayed cells, with prominences generally long and more regularly disposed than in the former, . .	Stellate parenchyma.
ELONGATED CELLS.		Cylindrical cells, with base abrupt or little pointed. (*Cellulæ conductrices*, Casp.)	
		Fusiform cells (*Clostres*, Dutr., *fibres* of other authors), . . .	Prosenchyma.

Single-celled Plants.—The majority of the higher plants are composed of numerous cells of one or more of the kinds just described. Others, such as fungi, algæ, lichens, &c., are composed of simple cells alone, and are hence known as cellular plants; while other plants lower down in the scale of existence consist of simply a single cell—the organs of life being here reduced to its simplest element, viz., *the* cell. And this cell performs all the functions which it is intended to fulfil just as well as in species more complexly organised. We find such in the red snow plant (*Hæmatococcus nivalis* of C. A. Agardh), which covers considerable tracts of the snow of the Alps and the Arctic regions. So rapidly does it increase, that in one night in the month of March the red snow plant covered a bank of snow to a considerable thickness. Each of these plants consists of a minute globule, distinct and separate, composed of a thin membrane perfectly closed in all its parts, colourless, but containing in the interior a red liquid. By-and-by granules appear in this red liquid, which grow and soon tear the envelope, and after a time give birth to other globular vesicles exactly resembling the mother cells. The same mode of growth can be seen in another species (*H. cruentus*), which covers with crimson stains the north side of damp walls. *Oscillatoria*, a minute plant which sometimes stains lakes of a greenish hue, is only an elongated single cell. Again *Vaucheria*, a fresh-water Alga, and *Bryopsis*, a marine one, are only single cells more or less branched. The "Zoospores" of all algæ, &c., are of this nature. The spores of Equisetaceæ are also single cells surrounded by

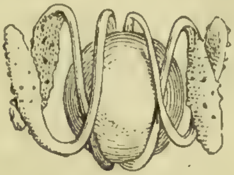


Fig. 9.—Spore of an Equisetum surrounded by its elaters.

curious bodies called Elaters (fig. 9). In *Botrydium* we see a cell branched, with some of the branches performing the function of a root to fix the minute plant in the mud. Here we see a tendency to a higher growth, where, as in moulds, the plant is composed of a series of cells—until we get on in the higher seaweeds to a plant composed of layers of cells, then to cells thickened in various ways to serve the purposes of hard tissue, until finally we see them altered to woody tissue, and vessels as in the higher plants.

Intercellular Canals.—Though most cells are united to the contiguous ones so closely as to leave no appreciable space between,[1] yet in various plants the cells only touch each other at one or two points, leaving, as in the green pulpy parenchyma, spaces between them, known as *intercellular canals*.[2] In some species of plants these are well marked, while in others they are so indistinct as to have led some authors to deny their existence. In shape they also vary much. Kieser and De Candolle look upon them as intended to contain sap, and even make them out to be true sap-vessels. The probability is, however, that they principally contain air. In the stems and leaves of most aquatic plants, such as rushes, Nymphæaceæ, &c., the intercellular canals are filled with air. In some cases, by the absorption of the cells which bound them, these canals can be increased in size. This is seen in the culm of grasses and in the stem of orchids.

Intercellular Substance.—The myriads of minute cells which in combination make up the parenchyma of the plant, are cemented together by a substance apparently secreted by them, and known as the *intercellular substance*.[3] Ordinarily it is found in a very thin layer between the cells, but in some cases where large intercellular canals are found, it exists in considerable quantity; and in *Nostoc*, and other low forms of Algæ, it exists as a jelly, in the midst of which the cells are found in the form of little strings. In *Chordaria scorpioïdes* and in *Fucus vesiculosus* (the bladder-wrack), two species of marine Algæ, Schacht found that the intercellular substance was the product of the decomposition of the walls of the cells. The cuticle of Algæ is of the same origin. In the cellular tissue of *Helleborus fœtidus* (fetid hellebore) and *Dipsacus fullonum* (fullers' teasel), it completely fills up the intervals between the cells, except the central part, which is sometimes

---

[1] The "perfect parenchyma" of Schleiden.

[2] *Meatus intercellulares;* hence called by Schleiden "imperfect parenchyma."

[3] "*Intercellular substanz*" of Mohl, who so named it in 1836.

occupied by a bubble of air. Iodine and sulphuric acid colour the walls of the cells blue, whilst the intercellular substance remains uncoloured; on heating the preparation in a solution of potash, the walls, composed of cellulose, swell up, while the intercellular substance does not: finally, while the cell-walls are rapidly destroyed by sulphuric acid, the intercellular substance resists that agent, though, according to Schultz, it disappears more quickly under maceration than the cell-wall. The intercellular substance is common to the two cells, which it unites; and so firmly does it cement them together, that the cell will tear before the intercellular substance will give way. It follows that, though we portray on paper the cells as being separated from each other by well-marked lines, these lines are to a great extent fictitious. For instance, in fig. 3, *a a*, the intercellular membrane is shown as interposed between double lines, the walls of two contiguous cells. In nature, however, the cells seem as if soldered together—as will be apparent from what we have said regarding the intimate union effected between them by means of this intercellular substance.[1]

Schacht, Wiegand, and others, seem to consider that the cuticle is simply the intercellular substance formed on the free surface of cells; but others are inclined to doubt the existence of the intercellular substance altogether, or its identity with cuticle. Relying on the behaviour of cellular tissue when coloured with carmine, Dr W. R. M'Nab believes that the "so-called intercellular substance is in reality the primary or cell wall—that as the growth goes on, this primary cell-wall becomes thickened by the addition of numerous more or less marked layers on the inside."[2] The subject is one of interest, but we cannot think, for many reasons, that the question is yet definitely settled.

Nature of the Cell-Wall.—We now come to consider what is the nature of the membrane which forms the walls of the cell. In its original form the membrane is thin, transparent, and colourless, with a pearly lustre; and if the tissue into which it enters is coloured, the colour is due to particles inside the cell, and not to the cell-wall. If the cells communicate with each other it must be by exosmose and endosmose, or by means of minute pores which we have not yet been able to detect, though such have been seen by some observers. In one cell from a *Euphorbia* (Spurgewort), Mülder and Harting saw forty-five exceedingly minute openings, though the whole transverse diameter of the cell was only 0.03777 of a millimetre.

Chemically considered, the cellular membrane is composed of

---

[1] Hartig appears to have mistaken this for a third coat of the cell-wall, common to two contiguous cells. He calls it *Eustathe*.

[2] Trans. Bot. Soc. Edin., x. 73, 315.

a substance which dissolves in sulphuric acid and swells in a solution of caustic potash. To the substance characterised by these reactions has been given the name of *Cellulose* ($C_6H_{10}O_5$). It is isomeric with starch and dextrine, and contains no nitrogen.[1] Pringsheim considered it a secretion of the *protoplasm*, or liquid which it envelops.

Markings on the Cell-Wall.—Up to a certain stage the cell-wall thickens *interstitially* by the incorporation of new matter into its substance, and then remains stationary—either thin or thick, according to its nature. Often, however, the cell-wall is thickened by deposits, which circumscribe the space inside into very small dimensions (figs. 10 and 11). In the stones of fruit, the shells of the Cocoa-nut, and suchlike structures, the whole interior is filled up with a hard deposit called *lignine* or *sclerogen*,[2] which is only a modification of cellulose. In others it is only deposited to a slight extent and remains soft. This thickening (or "secondary deposit") is due to the deposition of material, at first liquid, on the interior of the cell-wall,[3] in successive layers, so that a transverse section (fig. 10, *lb*, and fig. 11) shows a number of superimposed deposits firmly united together. It sometimes, however, happens, that after the first layer has been deposited, the second layer does not cover it, but is deposited in detached patches over it; the successive layers which follow take the same dis-

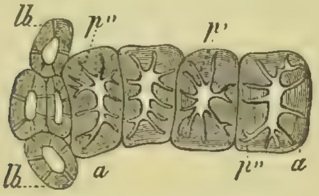


Fig. 10.—Section of some cells with thickened walls taken from an exotic Aristolochia (*A. cymbifera*, Mart.) The concentric lines (*a a*) seen in the walls indicate the superimposed layers of thickening matter; *p' p''* Hollow canaliculæ in the walls. Towards the left the same cells are seen (*lb lb*) in transverse section.

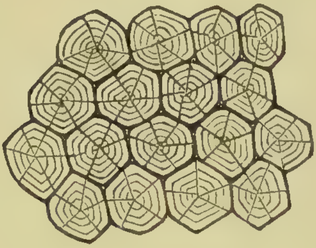


Fig. 11.—Transverse section of thickened cells from the pulp of the pear.

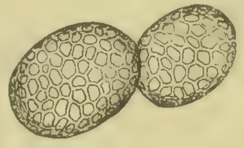


Fig. 12.—Two cells regularly and distinctly marked with little polygonal reticulations, from the endosperm of the seed of *Aristolochia clematis*, L.

---

[1] See Ultimate Constituents of the Plant, Chap. iv. Sect. ii., for the Chemistry of Cellulose.

[2] *Lignum*, wood; σκληρός, hard; and γεννάειν, to generate.

[3] Mohl and the greater number of observers believe this, but Hartig, Harting, and others, teach that the cell-wall is thickened by layers from without inwards, and hence this has been called the "centrifugal theory."

position,—so that, on looking at the cell, it seems as if covered over with punctations or slits, these apparent punctations being the imperfect deposits inside; and the slit-like appearances, longitudinal bars of a similar nature appearing through the still transparent cell-wall. The cell-wall is never perforated unless accidentally; such an appearance is only an optical illusion. We have spoken of these markings as "deposits." The student ought, however, to bear in mind that these are not due to a mechanical but to a vital process—in fact, that the process is a physiological one. To be brief—it seems that certain parts of the cell-membrane have the power of assimilating the nutritive material in its interior, and so thickening it, and that other portions have not this power, and accordingly remain in the primitive condition of the transparent membrane. Sometimes this deposit takes a spiral form, and these forms of deposit on the interior of the cell-walls are characteristic of particular tissues in particular orders or species of plants, which can be readily recognised by this means. The modifications of the cell-wall are, then, as follows:—

1. *Simple* (fig. 2): those transparent and without markings of any sort.

2. *Thickened* (figs. 10 and 11): concentric layers deposited in the interior, and united one to another (as seen in the stones of fruit, &c.)

3. *Punctated*, or dotted and disked (figs. 8 and 1). The first form is seen in the elder, plane, gourd, wheat, and other plants. The pits of contiguous cells exactly correspond. Though not previously pits, they often become so with age "by the destruction of the primary membrane after the cell has lost its vitality." Their use may be to convey sap from cell to cell, when the thickening of the walls might prevent this by the ordinary "endosmose" and "exosmose." The second kind of marking (viz., the disc) is found on firs, pines, and all the trees of that order, as well as on the winter bark (Drymis), Magnolia, &c. The regularity of the discs in the coniferæ is especially remarked—the markings on two contiguous cells being uniform; so that the disciform markings are in lines transversely and perpendicularly in the tissue. The nature of these areolæ has been studied with great care by Schacht,[1] Mohl,[2] Sanio, Dippel,[3] and others, with different results. In general terms it may be affirmed that what looks like dottings in this tissue is, in many cases, formed simply by crescentic depressions in the sides of two contiguous cells or vessels, the two in apposition forming between them a lenticular cavity, in the centre of which is a canal — frequently funnel-shaped — which,

---

[1] Botanische Zeitung, 1859, 283; De Maculis, &c., 1860; and in Ann. Sc. Nat., 1860.

[2] Die vegetabilische Zelle, 1851 (also English Trans. by Henfrey, 1852).

[3] Bot. Zeit., 1860.

owing to the thinness of the contiguous tube, gives the appearance of a second circle inside of it.

4. *Reticulated* (fig. 12), in which the markings form a more or less regular reticulation, as in the wing of the seed of *Swietenia* (mahogany), seed-vessel of *Picridium tingitanum* (a Tangiers plant belonging to the order Compositæ, common in our gardens), pith of *Rubus odoratus* (an American bramble cultivated in this country), &c.

5. *Annular* or *ringed*, as in *Opuntia*.

6. *Transversely barred*—in short, incomplete bars; hence called "scaliform," or barred like the rungs of a ladder (elder, &c.)

7. *Spirally marked*, composed of one or more bands or filaments rolled in a spiral manner, as in the leaves of various Orchids (*Oncidium*, *Pleurothallis*), also in Balsam, leaf of *Sphagnum* (moss), &c., and in the spore-cases of various Cryptogams. Further examples are afforded by the spirally-lined hairs which cover the coats of the seeds and seed-like fruits of *Acanthodium spicatum*, *Sphenogyne speciosa*, and species of *Collomia*, *Gilia*, *Senecio* (groundsel), *Crocidium*, *Salvia* (sage), &c., the filaments from which exhibit movements when placed in water, probably only due simply to elasticity from the absorption of fluid. When the wall is very thin, then the spiral marking is apt to be left as a separate thread by the obliteration at maturity of the wall. This, as Gray has remarked, occurs in the tissue that lines the walls of the anther; and the spirally-marked tubes (*Elaters*) of the spore-cases of *Hepaticæ* (fig. 9) are converted by this means into elastic spiral threads.

Fig. 13.—The pointed extremities of two imperfect tracheary vessels from the stem of the garden balsam (*Balsamina hortensis*, Desp.), applied against each other.

The reticulated, annular, and spiral cells are often called "fibrous cells,"[1] forming as they do the woody or fibrous tissue.

The different tissues formed from these cells, or fibre-cells, will be considered when we come to speak of vascular tissue.

Contents of Cells.—Many cells, such as those of the epidermis, pith, bark, &c., are often empty or filled with air, but all true living cells are filled with liquid and other contents. These contents may be divided into—1. Gaseous; 2. Liquid; 3. Solid. Under these heads we shall therefore consider them.

1. The *Gaseous Contents* are chiefly air, more or less altered.

2. *The Liquids* contained in cells are somewhat more complex. First in importance ought to be mentioned the *protoplasm*, a

---

[1] Or in mass "fibrocellular tissue," or *Inenchyma*, (ινες, fibres). See Purkinje, "De Cellulis antherarum fibrosis" (1830), in which memoir attention was first called to them; and the subsequent papers of Slack (Ann. des Sc. Nat., i. 195); Schleiden and Horkel (ibid., 1839), Mirbel, &c.

granular viscid substance, composed of *proteine* and rich in nitrogen, and surrounding the *nucleus*. It chiefly occupies the interior of young cells, which it often fills entirely. The *primordial vesicle*, an extremely fine membrane, separates this protoplasm from the other liquids contained in the cell.

Gyration in Cells.—In some plants the granules of the protoplasm keep up a gyratory motion within its containing membrane —*e. g.*, in the cells of *Chara*, *Caulinia*, *Nitella*, *Naias*, *Anacharis*, *Hydrocharis*, *Vallisneria*, the hairs and stamens of *Tradescantia*,[1] in the hairs of the *Cucurbita*, Galeopsis, Borage, nettle, plantain—indeed nearly all hairs, the cells of the cotyledons of the seed of the common walnut, &c. This is called *Rotation* or *Gyration*, and was described in 1774 by Bonaventura Corti of Modena, though since that time the phenomenon has been the subject of numerous memoirs by Treviranus, Schultze, Amici, Poiseuille, Donné, Dutrochet, Slack, Branson, &c. It can be seen, in the hairs of *Tradescantia* (the Virginian spider-lily), in thread-like currents traversing the cell in various indeterminate directions. In the bristles on the ovary of *Circæa*, the current flows regularly up one side of the cell, round the top, and down the other side. In *Chara* and *Nitella* the circulation is also seen with lower power (50-100 diameters) of the microscope. In *Vallisneria spiralis*, as seen with from 2-400 diameters, it describes a complete course round the cell, often carrying granules of chlorophyll with it, and even setting free the nucleus in its course. It is retarded by cold and accelerated by moderate warmth, though heat above 150° Fahr. stops it; a current of electricity also stops it; but no sooner is the current shut off than it recommences. Any mechanical irritation, such as jolting, pricking, &c., also stops it. Putting *Vallisneria* in milk or a thin solution of gum accelerates the gyration in that plant. The circulation in one cell is independent of that in the others, even contiguous cells.

Speed of the Currents.—The speed of these currents has been calculated by Mohl at $\frac{1}{1857}$ of a line per second in the hairs of the cucumber; $\frac{1}{700}$ of a line in the hair of the nettle; $\frac{1}{500}$ of a line in the *Tradescantia virginica;* and $\frac{1}{183}$ of a line in the leaves of *Vallisneria spiralis*.[2] However, in the latter plant the current has been observed to describe the circuit of the cell in less than 20 seconds, and in the bristles of the ovary of *Circæa*, which are half a line long, Mr H. J. Clark has seen the revolution completed in a minute.

Cause of the Gyration.—This is very unsatisfactorily known. Cohn, Unger, and more recently Max Schulze,[3] have expressed a belief that it is due to vital contractility—the idea that it is effected

---

[1] Wenham in Quart. Journ. Mic. Sc., iv. 44.

[2] Bot. Zeit., 1846, Col. 92.

[3] Das Protoplasma der Rhizopoden und d. Pflanzen—Zellen, 1863.

by "cilia," or minute lashes attached to the sides of the cells, being discarded as originating in an optical illusion.[1] It has been supposed by some physiologists that they have detected on the inner wall of the cell a series of exceedingly minute anastomosing vessels in which the gyration is performed; and Slack[2] has described the existence of a second cell within the first, and attached here and there to it, but leaving a narrow space between the two, in which the gyration goes on. Dr J. Bell Pettigrew considered that he had proved, by his producing these gyratory movements artificially by means of an ingenious apparatus, that they were chiefly caused "by *absorption* on one hand, resulting in endosmosis and exosmosis; and *evaporation* on the other."[3] This idea is not improbable; and possibly the effect of lead, opium, corrosive sublimate, prussic acid, alcohol, &c., in stopping the gyration, may be due to the well-known fact that all acids, alkalies, soluble salts, alcohol, &c., on account of their liability to enter into combination with the permeable organic membrane, destroy endosmosis. We should, however, remember, that gyration in cells is not a general phenomenon in plants, as we should expect to find it if this explanation of the able and justly eminent physiologist quoted was correct.

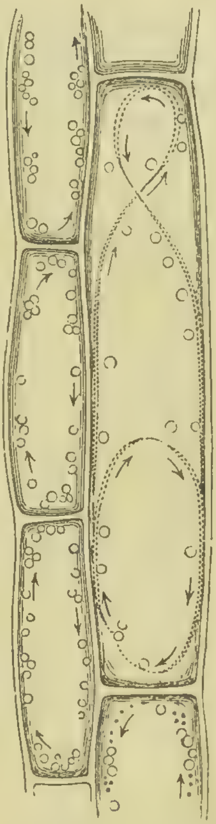


Fig. 14.—A few cells of the leaf of *Naias flexilis*, highly magnified, showing the intercellular circulation, the direction of the currents indicated by arrow-heads (after Gray.)

It is not unlikely that gyration may be a much more universal phenomenon, especially in early cell-life, than we have hitherto supposed. Max Schulze observed in the pseudopodia of *Amœba porrecta*, a protozoan animal, a similar current to that in the cells of the cotyledons of the walnut. Lastly, Professor J. B. Schnetzler records some observations on the motions of the fluid in the leaves of the common water-weed *Anacharis alsinastrum*, introduced from America some fifteen years since, and now known in this country as a great pest in our canals and rivers, which the great transparency of the leaves renders peculiarly favourable for examination. These rotatory motions of the protoplasm have, in addition to the explanations mentioned above as being proposed, been attributed by some to successive contractions of the exterior layer of the cells, by others

---

[1] Branson in Quart. Journ. Mic. Sc., ii. (1854) 131.

[2] Ann. des Sc. Nat., 2d ser., i. 193.

[3] Lectures on the Circulation: Edin. Med. Journ., 1872, 98.

to successive displacements produced by purely mechanical action. Neither of these explanations, Professor Schnetzler points out, goes to the root of the matter; and he believes that he has detected their ultimate cause in the chemical action of oxygen, which passes through the wall of the cells, and of which a portion is probably transformed into ozone under the influence of light, assisted by currents of electricity passing between the surface of the leaf and the contents of the cell. A similar conversion of oxygen into ozone is said to take place in the globules of the blood of animals. From the point of view of the mechanical theory, we have here evidently an example of the transformation of light and of heat into motion.[1] The question as to how these strange gyratory movements in the cells of plants are caused is therefore still *sub judice.*

The cell-liquid proper is a juice rarely altogether colourless, the colour being probably derived from the solid cell-contents, of which we have to speak presently. Sometimes the place of the water is taken by oils secreted by the cell; it disappears in old wood-cells, and air takes its place in cork.

It is capable of holding in solution very different and varied substances, such as gums and sugars.

3. *Solid Materials.*—These are very important and numerous, and play an important part in the nutrition of the plant. They are chiefly the *nucleus*, *chlorophyll*, *starch*, and *crystals.*

(*a*) *The Nucleus.*—We always find in the interior of young cells a lenticular or irregularly globose body, applied to a point on their sides in the midst of the protoplasm, to which the name of *nucleus* or kernel has been given. Schleiden, on account of the belief common among many physiologists that it plays an important part in the production of young cells, has called it the *cytoblast*, and describes it as composed of a number of extremely little corpuscles of indeterminate form. These he calls *nucleoli*, and according to this celebrated observer each *nucleolus* is a rudimentary cell. The nucleus, Schleiden affirms, is found in all young cells; it gets atrophied during the progress of growth, and in a number of cells is wanting altogether. On the contrary, Unger[2] and Richard[3] believe that the nucleus does not exist in very young cells, and that it only commences to show itself at a late period of the cell's existence. In orchids, in which order Robert Brown showed it for the first time, the nucleus is very well seen; and in the leaves of *Orontium japonicum* it is sufficient to cause elevated markings on the epidermis, each subjacent cell having a well-marked nucleus. It can be easily seen, especially if a little iodine is applied. In that case it takes a marked brown colour, and shows distinctly that it is composed of irregu-

---

[1] The Academy, 1869, 47.

[2] Ann. des Sc. Nat., xvii. 232.

[3] Noveaux Eléments de Botanique, 10th ed. 9.

larly round transparent globules, though we do not yet know whether they are really globules or little cells—solid or empty.

Dujardin[1] has put forth another opinion on the origin and functions of the nucleus, different from that of Schleiden. According to him, this body results from the condensation of the protoplasm, which fills the interior of the cells, and does not serve the important purposes that many phytotomists would ascribe to it—in a word, he holds that there is no reason to believe that it is concerned in the formation of new cells. This doctrine, though held by some physiologists, is scarcely consistent with observed facts.

(β) *Chlorophyll.*[2]—This peculiar substance is found in all parts of the cellular tissue having a green colour—the green colour of the tissue being due to the fact that the colour of the granules can be seen through the thin transparent cell-wall. It especially abounds in leaves,[3] and has been shown by Mohl to be present in two forms—viz., round or ovoid grains or granules, and in a gelatinous shapeless mass, in which are scattered granules of starch. The granules or masses float loose in the cell or are united to the sides. Some observers consider that the granules are colourless in themselves, but get coloured by a semi-liquid substance deposited on their surfaces. Alcohol decolourises chlorophyll by dissolving the resinous matter; hence flowers and leaves, if plunged into alcohol, are quickly blanched. Amorphous chlorophyll is usually found in the shape of little gelatinous or flocculent masses, or of filaments adhering to the sides of cells; but in some of the simpler Algæ, *Mongeotia genuflexa*, *Conferva zonata*, *Zygnema*, &c., it is found in bands or lines of a remarkable character. In the last-mentioned genus it is in the form of a spiral against the wall of the cylindrical cell.

Chlorophyll, however, generally exists in cells in the granular form. These granules are very small—from $\frac{1}{133}$ to $\frac{1}{111}$ of a millimetre in diameter,[4] and often hexagonal from mutual pressure. The external layer of these granules is not, however, a special membrane, and has nothing of the nature of a true vesicle,[5] though a contrary opinion has been held by some botanists of eminence,[6] who even went so far as to consider the chlorophyll granules destined to develop true cells. On the whole, after sift-

---

[1] Observations au microscope, 202; cited by Richard, *op. cit.*, 9.

[2] Chromule of De Candolle (from χρῶμα, colour).

[3] Hence the somewhat inappropriate but familiar name *Chlorophyll* (χλωρός, green; and φύλλον, leaf), given in 1818 by Pelletier and Caventon to this substance.

[4] Mohl in Ann. des. Sc. Nat., 1838, 1855; Boehm in Sitzungsberichte der Akad. Wien, &c., 1857; Berzelius, Ann. des Sc. Nat., 1850.

[5] Morren, Dissert. sur les feuilles vertes et col., 1858; Gris in Ann. des Sc. Nat., 1857.

[6] Turpin (1828), Raspail (1837), Meyen (1830, though in 1837 he abandoned that doctrine), Mirbel (1831), Naegli, Trecul (1858), and others.

ing the various contradictory opinions evolved in the voluminous literature of which chlorophyll has been the theme, we are inclined to agree with the opinion of M. Duchartre that it "affects a series of states connected with and passing into each other," and that "the jelly-like condition of the granular form can change into the amorphous by the granules acquiring a greater consistence and being confined within a false envelope." The chemical characters of chlorophyll will be given when treating of the chemical constituents of plants.

Sachs has shown[1] that the intensity of the colour of chlorophyll diminishes under the direct influence of the sun's rays; but by the researches of Famintzin,[2] Borodin,[3] Prilleux,[4] and Roze,[5] it has been shown that this change of colour is only apparent, and results from certain movements performed by the granules in the interior of the cell. During the day the granules group themselves in the cells along the horizontal walls or those parallel to the surface; but during the night they execute a movement of retreat and place themselves along the walls perpendicular to the surface. Light, and not heat, is the cause of this phenomenon. The most refrangible rays alone have the power of drawing the chlorophyll towards the surface, the most luminous rays producing the same effect as complete darkness.

These movements must necessarily, from the anatomical relations of the different parts of the cell, be accompanied by a displacement of the whole protoplasmic mass.

Frank,[6] from observations made on *Sagittaria sagittifolia* and *Mnium rostratum* (Schivægr.), came to the conclusion that chlorophyll, in addition to the properties described, has a "tendency to move in the interior of the cell to the side which is most illuminated, exactly as zoospores (or the free-moving seed-like bodies of certain algæ) do when placed in a plate near a window." Though the position, orientation, or direction of the cells has no influence on this phenomenon—it being as well manifested in diffused light as in the sun's rays—"in a general way diminution of the intensity of the light renders the phenomenon less striking and sometimes irregular; it is, however, always manifested, whatever may be the colour of the luminous rays." It is probably associated with peculiar protoplasmic intracellular currents.

It has now been shown that we must greatly modify our old belief in the most luminous rays of the spectrum alone acting in the phenomena of assimilation. This is a subject so important that even in elementary studies some knowledge of the recent

---

[1] Physiologie Végétale (Fr. Trans.), 16.

[2] Pringsheim's Jahrbuch für wiss Botanik, v. 49.

[3] Mélanges Biologiques tirés de l'Acad. Imp. de St Petersburg, vii. (1869), 50; and Bot. Zeit., 1869, No. 38.

[4] Comptes rendus, 1870, lxx. [5] Ibid. [6] Bot. Zeit., 1871, No. 14.

researches in regard to it ought to be acquired by the student. Gregor Krauss,[1] Prilleux,[2] and Baranetzky,[3] particularly the latter, have made investigations in regard to this question, and the state of knowledge regarding it may be summed up as follows, viz., that — (*a*) The decomposition of carbonic acid (CO_2) or assimilation, the formation of chlorophyll, and the destruction of the colouring principle, are phenomena solely dependent on the degree of luminous intensity; (*β*) "heliotropic curvatures"—*i.e.*, the movements which certain plants, like the sun-flower, perform under the influence of the sun—the periodical movements of organs, the currents of protoplasm, and the changes of place of the grains of chlorophyll, are executed only under the influence of the most refrangible rays.

From the observations of Mr H. L. Smith there seem some grounds for believing that the endochrome of the microscopic aquatic plants known as "diatoms" is identical with chlorophyll. Lastly, chlorophyll is not confined to the vegetable kingdom; a green colouring matter closely allied to, if not identical with it, may be detected in many animals belonging to the sub-kingdom Protozoa, &c.

Its origin has been the subject of careful research by Quekett,[4] Mohl,[5] Gris,[6] and Trecul,[7] but it is still more a matter of speculation than of ascertained fact, the general belief being that it is either derived from the nucleus in a manner analogous to that in which starch is, or that it is a transformation of the protoplasm—the last view being that of Mohl and Trecul, while Quekett and Gris are the authorities for the former opinion.

(γ) *Starch.*[8]—Fecula or starch is one of the most important and generally diffused of cell-contents, and one which renders plants so valuable as the food of many animals. In a dry state, it presents itself in the form of a white powder composed of little grains, set free by the rupture of the membrane of the cell containing them. It is found in a variety of plants. In the records of economic botany are enumerated many such—more or less familiar in domestic or commercial economy. Among seeds abounding in starch may be mentioned the whole order of the Gramineæ or grasses, more especially those species known as cereals: such as wheat, barley, rye, oats, maize or Indian corn (*Zea Mays*, L.), rice (*Oryza sativa*, L.); various cereals of Africa, such as "teff" (*Poa abyssinica*, Jacq.), "dourra" (*Sorghum*), the "toucusso"

---

[1] Pringsheim's Jahrb., vii. 511.

[2] Comptes rendus, 1870, lxx. 521; Ann. des Sc. Nat. 5e sér. x.

[3] Bot. Zeit., 1871, No. 13.

[4] Annals of Nat. Hist. 1846.

[5] Vegetable Cell, &c.

[6] Ann. des Sc. Nat. 1857, cited in Bull. Bot. Soc. Fr. 1857, 154-156.

[7] Ann. des Sc. Nat. 1858.

[8] Cells containing it in tissue received the name of *Perenchyma* (πηρα, a sac) from Charles Morren.

(*Eleusine Tocusso*, Fres.); the Natchanee or Murooa of the Hindoos (*Eleusine coracana*, Gært.), millet, Bujera or Bujra of the Hindoos (*Penicellaria spicata* W.), &c. Starch is also found in the following plants cultivated for their edible seeds: Buckwheat (*Fagopyrum esculenteum*, Mænch, and *F. tartaricum*, Gært.), quinoa (*Chenopodium Quinoa*, L.), and two or three Amaranths very little known (*Amarantus frumentaceus*, Buchan.; *A. farinaceus*, Roxb.; *A. Anardhana*, Royle). It is the starch which gives the value to the seeds of various leguminous plants, such as haricots (*Phaseolus*), peas (*Pisum sativum*, L.), lentils (*Ervum Lens*, L.), beans (*Faba vulgaris*, Mænch), chick pea (*Cicer arietinum*), *Dolichos*, &c.; also the chestnut (*Castanea*) and various other trees.

It ought also to be mentioned that in most of these plants, and especially among the cereals, the starch is mixed with nitrogenous matter, which renders them more nutritious than they would otherwise be. The fruit of the banana (*Musa*) contains, before being ripe, starch, which is replaced at that period by sugar. In the stems of some plants starch accumulates, especially towards the centre. For instance, sago is obtained from the pith of the sago-palm (*Metroxylon Rumphii* and *M. læve*) of the Malay Islands,—a single tree of which will sometimes yield 800 pounds; *Caryota urens*, L., *Cyas revoluta*, Thim., and *C. circinalis*, L.: little of the sago derived from the three latter ever comes to this country, being mostly consumed on the spot.

In the parts of plants which are situated beneath the surface of the ground starch also accumulates, for the nutrition of the plant. Among such plants we have to enumerate the well-known potato (*Solanum tuberosum*, L.); the sweet-potato (*Batatas edulis*, Choisy); yams (*Dioscorea alata*, L.; *D. Batatas*, Dcne., &c.); colocasia or kuchoo of the Hindoos (*Colocasia antiquorum*, Schott); taro or tara of the Polynesians (*Colocasia esculentea*, Schott); Pia (*Tacca pinnatifida*, Forst.); Manioc (*Manihot Aipi*, Pohl.; *M. utilissima*, Pohl.) This latter species furnishes tapioca, while *M. arundinacea*, and *M. ramocissima*, L., West Indian species, furnishes the chief portion of the arrowroot of commerce.[1]

"Tous les mois" is got from the tuber of a species of *Canna*,—probably *C. edulis*.

Finally, we may mention that starch is not confined to the vegetable kingdom, being, at all events, found in the lowly-organised animals known as the *Radiolaria*.[2]

In *form* starch-grains are well marked, consisting of a dot or *hilum*, generally near the smaller end, with concentric lines drawn around it. The shape of the grain differs in every different species

---

[1] Julius Munter showed (Bot. Zeit., 1845, No. 12) that under the common name of "arrowroot" are imported the starch of at least three species of plants, each easily distinguished by the characteristic form of their grains.

[2] Haeckel—"Beiträge zur Plastiden Theorie"—Jenaische Zeitschrift, v.

of plant in which it is found. The grains are generally rounded or oval, but sometimes angular from mutual pressure. In the tissues starch is rarely found in an amorphous state, but generally in the form of separate grains, each possessing the characters above mentioned. The starch-grains and their mode of formation have, since the days of Leeuwenhoek down to our own, been a fertile subject of observation and opinion,—more frequently of opinion without observation at all. Notwithstanding that microscopists of the eminence of Raspail, Payen, and Trecul, in France; Busk, Allman, Cruger, Grunde, Henfrey, and Rainy, in England; and Fritzche, Schleiden, (above all) Naegli and Munter, in Germany,—have given their attention to it, we are yet far from having very clear ideas in regard to the subject. Our space forbids to enter upon this discussion, nor will the student lose much by the omission. One fact tolerably well established regarding starch is—that its presence is a criterion of the age of the plant, the vital activity of the cell being at an end after this substance is developed.

Regarding the mode in which starch is *produced* in the interior of the vegetable cell, Trecul and Gris have made researches,—the result of which is that it seems to be excreted by the protoplasmic material contained in the cells—*i. e.*, either by the primordial utricle, by the filaments of protoplasm, or directly or indirectly by the cell-nucleus. The lines shown on the surface of a grain of starch are evidently marks of the deposition of layers around a central nucleus (the "dot" or *hilum*), which is usually very excentric, owing to the deposits being thicker on one side than on the other.

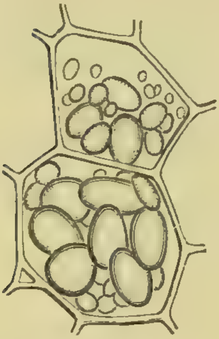


Fig. 15.—Two cells of a potato-tuber, containing starch-grains.

Fig. 16.—A grain of starch from the potato; *h* Central point or *hilum*; *a b* The two extremities of the granule, the last of which (*b*) is very excentric.

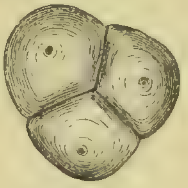


Fig. 17.—Accidental form of starch-grains in the potato. Here three simple grains are united into one.

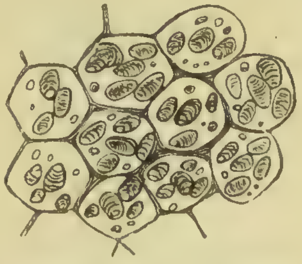


Fig. 18.—Section of cellular tissue containing starch-grains (from the seed of maize or Indian corn).

It appears that before starch can be fitted for the nutrition of the plant, it must be converted through the agency of diastase into dextrine, as it cannot dissolve in cold water, and hence not in the juices of the plant.

A chemical test for starch is its giving a beautiful blue or purple colour when acted on with iodine.

The *shape* of the starch-grains, we have already mentioned, varies much. The following table, compiled from Duchartre,[1] shows the chief forms of the starch-grain, which it is all-essential for the botanical student to be acquainted with, so that he may recognise them under the microscope :—

A. Grains simple.	Contour, oval or rounded.	Without visible nucleus.	Very small, rounded. *Ex.* Throughout nearly all plants, but especially in wood in winter.
		Nucleus small and rounded.	Large, ovoid, generally rather straight towards the tip. *Ex.* Potato (fig. 16).
		Nucleus elongated and branched.	Small or large, oval, a little depressed. *Ex.* Haricot, Pea, Bean.
		Angular or polyhedral.	Polyhedral, more or less rounded on one side. *Ex.* Maize (fig. 18). Very small, polyhedral, with marked ridges. *Ex.* Rice.
B. Composite grains.		Without visible nucleus.	Formed of two to four elementary grains with a small rounded nucleus. *Ex.* Tapioca.
		With a visible nucleus.	Formed of many elementary grains disposed round a greater. *Ex.* Sago.

In *size* starch-grains also differ much, and, as might be expected, often differ much in the same plant.

Payen has given a table of the sizes of the starch-grains of various plants, from which the following are selected :—

Various kinds of potato from	.185—.140th	of a	millimetre.
Arrowroot of *Maranta arundinacea*	.140	"	"
Various sagos	.070—.045	"	"
Large garden-bean	.075	"	"
Lentil	.067	"	"
Haricot	.063	"	"
Seed of Maize	.030	"	"
Seed of Millet[2]	.010	"	"
Seed of Beet[3]	.004	"	"
Seed of Quinoa[4]	.002	"	"

Innline and *Aleurone* are only other forms of starch, and will be noted more particularly when we speak of the "Ultimate Constituents of Plants."

To recapitulate—the contents of the cells may be put in tabular form as follows, classifying them according to their *chemical*

---

[1] See also the researches of Rivot and Moitessier in Annales de physique et de chemie, 3e série, lxvii. ; and Mém. de l'Académie de Montpellier, vi. 336.

[2] *Panicum miliaceum.*

[3] *Beta vulgaris*, var. *rapacea.*

[4] *Chenopodium Quinoa.*

constitution, though for convenience' sake we have considered them in the foregoing pages according to their *physical* character :—

1. Organic.	Non-nitrogenous.	Neutral	Starch, inuline, gums, sugars, &c.
		Oxygenised	Vegetable acids, pectine, and pectose.
		Hydrogenised	Oils, resins, wax, &c.
		Hydrocarbons	Essential oils of turpentine, orange, citron, &c.
	Nitrogenous.	Neutral	Aleurone, albumen, legumine, glutine, fibrine.
		Non-neutral	Alkaloids, chlorophyll, colouring materials.
2. Inorganic.		Salts (dissolved or crystallised)	Carbonates, oxalates, chlorates, malates, tartrates, &c., of lime, potash, &c.
		Acids	Silicic, oxalic, carbonic, &c.[1]

In the progress of growth the contents change, one substance disappearing and another taking its place; again, during the germination of the seed changes take place, oxygen being absorbed, and the insoluble starch and oil passing in a state of solution to serve as food for the young plant.

(δ) *Crystals.*—In the interior of the cells are also found crystals of a perfect and determinate form, sometimes isolated, at other times united in masses of greater or less size. They are found in the shape of rhomboids, cubes, octohedrons, or prisms. Sometimes the cells which contain them do not differ from the rest of the parenchyma; at other times they are manifestly larger. They are found in more or less abundance in all plants, but are more plentiful in the cells of the leaves and bark, and in the wood and pith of herbaceous plants. In an old stem of the "old-man cactus" (*Cactus senilis*), according to Gray, 80 per cent of the solid matter was found to consist of crystals, rendering it almost as brittle as glass: and in the inner layer of the locust-bark each cell contains a single crystal. The late Professor Bailey, of the U.S. Military Academy at West Point, calculated that "in a square inch of a piece of the locust-bark, no thicker than ordinary writing-paper, there are more than a million of these crystals."

(1.) One form common in plants belonging to various orders is that known under the name of *Raphides* (D.C.)[2] They consist of sharp needle-shaped bundles of prisms, commonly of oxalate of lime, though carbonate, sulphate, or phosphate of lime not unfrequently enters into their composition, terminating each in a fine pyramidal point[3]—one cell often containing them in considerable numbers (fig. 19.) The cells in which these crystals are found are very often without chlorophyll or starch. They may be seen to the extent of from 30 to 40 per cent in the cells of the stalk

---

[1] For further information on these cell-contents not already described, see Chap. iv. Sect. ii.

[2] 'Ραφὶς, a needle.

[3] Kieser, Organ. des Plant., 94, 122. Kieser was the first to point out their crystalline nature.

of the rhubarb (giving sign of their presence by grittiness of the tissue when cut through), the *Calla*, &c.

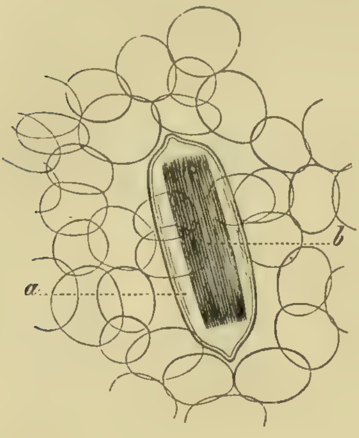


Fig. 19.—Raphides in a cell of *Colocasia antiquorum*. A cell, *a*, made larger than those which surround it, containing these *raphides* or crystals of oxalate of lime (*b*).

(2.) In the screw-pine (*Pandanus utilis*), the stem of which is remarkable on account of containing vessels belonging to the scalariform type, though otherwise resembling that of the palm, in addition to raphides in the cells of the cortex, &c., crystals of a peculiar type are found in connection with the fibro-vascular bundles. These crystals are contained each in a square-shaped cell, forming part of a string or chain. A number of these chains or strings are distributed round the circumference of each fibro-vascular bundle; they are especially abundant in its cortical continuation, as they do not suffer a degradation proportionate to that of the other constituent tissues. Mr Thissleton Dyer, to whom we are indebted for this curious observation, thinks that this arrangement of crystal-bearing cells is probably unique. The crystals are four-sided prisms with pyramidal apices. They are almost certainly composed of oxalate of lime, though they are too minute, and isolated with too much difficulty, to allow of their satisfactory examination.[1]

(3.) In fig. 20 is portrayed another group of crystals, common enough in various plants.

Weddell has applied the name of *cystolithes*[2] to these curious crystalline bodies generally found in the superficial cells of nettles and some other species of the order *Urticaceæ* and various genera of *Acanthaceæ*. Since they were first discovered (in *Ficus elastica*, Rox.) by Meyen in 1827, they have given rise to some difference of opinion regarding their nature.[3] They are globular or club-shaped bodies, or of various other forms, "usually hanging by a short stalk in an enlarged cell; their principal mass is found to be cellulose, but their surface is studded with crystalline points of carbonate of lime." Not only are the crystalline contents of cells enclosed by the general cell-wall, but they are covered by an extremely delicate organic covering closely applied to every part.

---

[1] Dyer in Report Brit. Assoc. (Trans. of Sect.), 1871, 128.

[2] Κύστις, bladder; and λίθος, stone.

[3] Besides their original describer Meyen, Payen, Schleiden, Weddell, Gottsche, and Schacht have all prominently shared in the controversy.

It only now remains for us to note the remarkable excretions (?) of carbonate of lime which form on the leaves of *Saxifraga Aizoon*, L., the silex in the stems of various species of plants, the tabascheer or deposit of silex in the hollow stem of the bamboo, &c. These can, however, be scarcely classed as cell-contents, and are noticed more in detail in their proper place.

Fig. 20.—A cell, taken from *Aristolochia Sipho*, containing a mass, *cr*, of united crystals or cystolithes, only showing their free extremities.

It may be asked—how do these crystals form in the interior of cells? In reply to this question, it may in the first place be pointed out, that acids of various kinds are formed in the plant, and that bases are taken up by the roots in the nutritive juices derived from the earth, and that the reaction of the one upon the other might produce such crystals of insoluble salts (carbonate and oxalate of lime). In proof of the probable truth of this explanation it may be pointed out that the late Prof. Quekett artificially produced raphides within the cells of rice-paper (pith of *Aralia papyrifera*) by first filling them with lime-water and then placing the paper in weak solutions of phosphoric and oxalic acids—the artificial crystal agreeing in crystalline form with the natural one of the same chemical composition, those of phosphate of lime being rhomboidal, while oxalate of lime crystallised into stellate forms. Allowing, then, that this is the source of these crystals, where does the thin organic envelope which covers them in the cell come from? In default of a better explanation Richard's may be received. He thinks that after the crystal has formed in the midst of the nutritive fluid of the cell, little by little a deposit of organic matter is applied to its surface until it is entirely covered. No other explanation can account for the existence of such a delicate membrane covering in such a close manner so many crystals as are found in the interior of a cell.

Lacunæ in Cellular Tissue.—In the cellular tissue are often found a number of lacunæ or cavities formed by the separation of cells, and the tearing, absorption, or partial destruction of the tissue. The most familiar examples of such lacunæ are afforded by the hollow stems of grasses and other plants, the pith of the walnut and other trees in which the tissue is found in the form of disciform transverse partitions, and in the floating leaves of water-plants. Sometimes these lacunæ are regular, at other times very irregular in form, and though generally filled with air, sometimes resin occupies their interior. To lacunæ, produced simply by the amplification of the intercellular spaces and the separation of the cells without tearing, Meyen and Leitgib[1] have applied the name of *Air-bearing Canals*.[2] They are so common, and occupy such a portion of the mass of the leaves of aquatic plants, that, ac-

---

[1] Sitzungsberichte, &c., 1856.

[2] *Luftgænge* in German.

cording to Unger, there are 713 parts of air in volume in 1000 of the substance of *Pistia Texensis*. They are also very regular in shape—passing continuously in a longitudinal direction through the substance of the leaf, as in fig. 21, showing a number of these in a transverse section of the common sea-grass (*Zostera marina*), a marine flowering plant, or in *Cymodocea æquorea*. They increase with the increase in length of the leaf.

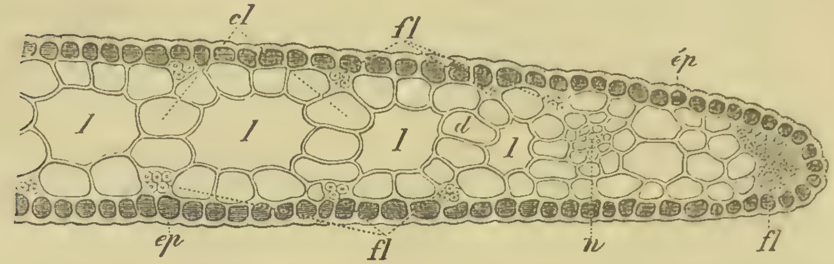


Fig. 21.—Transverse section of a portion of the leaf of *Zostera marina*, L., showing the range of air-bearing lacunæ. *l l l l* Separated by partitions, *cl*, formed of a single tier of cells; *n* Nerves; *ep* Epidermis; *fl fl fl* Bundles of very long cells.

To the spaces produced by the tearing, absorption, and destruction of tissue, the authors named have applied the special designation of *Air-bearing lacunæ*.[1] Unlike the air-bearing canals, these *lacunæ* do not appear in the early stages of the plant, and increase with the growth of the surrounding parts, or indeed are subject to any special laws of growth. In a word, they may be said to be *accidental*. They are seen in the stems of gramineæ, reeds, and similar plants. The leaves of many bulbous plants are also, apparently for the sake of lightness, full of such cavities—*e.g.*, those of the hyacinth. Leitgib has even divided these "air-bearing lacunæ" into two subdivisions: (*a*) *Canaliform lacunæ*, when they are somewhat long and continuous, and give passage to air; and (*β*) *Lacunæ, properly so called*, when perfectly isolated in the middle of the tissue, and often superimposed in lines or separated one from the other by transverse partitions. These distinctions cannot, however, be precisely applied to organs so variable. In the genus *Jussiæa*, particularly in *J. repens*, the lacunæ are very well marked in the roots, which here subserve the purposes of floats. In these species, Martins and Moitessier state the composition of the contained air to be 7 to 14 per cent of oxygen, and 86 to 93 per cent of nitrogen—a composition different from that of atmospheric air (nitrogen 79, oxygen 21 per cent).

---

[1] *Luftlücken* in German.

DEVELOPMENT AND INCREASE OF CELLULAR TISSUE (CYTOGENESIS).[1]

Having sketched out the character of the parenchyma formed by the union of cells, the student is now better able to understand the current doctrines regarding the development and increase of cells resulting in the formation of this tissue.

That these cells are very minute he will have already understood. In size, however, they vary much, even in the same organ, their ordinary diameter being between $\frac{1}{240}$ and $\frac{1}{1200}$ of an inch, though those of the gourd are $\frac{1}{30}$ of an inch in diameter, those of the lemon more than $\frac{1}{2}$ an inch in length, and those of the shaddock much larger.[2] *Caulerpa prolifera*, a marine Alga, though often a foot in length and branched into what look like leaves and roots, is in reality only a single cell; while in *Vaucheria*, *Bryopsis*, and *Chara*, the cells of the stem attain the length of several inches and a diameter of one-third of a line or more. The hairs which constitute "cotton" are single filamentous cells one to two inches in length. Again, the spores or dust-like seed-bodies of fungi are much smaller than any of those we have mentioned—the smallest of them allowing as many as 1728 millions within the compass of a cubic inch, each being not more than $\frac{1}{500}$ of an inch in diameter. That the rate of the production of cells is inconceivably rapid may be imagined from the fact that the flower-stalks of *Agave* or Century plant are said to increase in the humid tropics at the rate of about two feet per day. Mushrooms of gigantic size will spring up in a single night: the large puff-ball *(Bovista gigantea)* is calculated to develop at the rate of three or four hundred million cells per hour, though it ought to be remembered that the rapid increase of this plant is owing chiefly to the expansion of cells already formed.

The cell is in reality a complete living organism, capable of performing all the functions of life within itself; and the plant is either composed of one (p. 14) or of many such organisms in combination. We have already seen what the cell, in general terms, consists of. Looking at it from an anatomical point of view, we see that in a state of vitality it consists of—1. The *cell-wall*, already described (p. 16); 2. The *primordial vesicle*[3] (*utricle* of Mohl), a delicate mucilaginous film lining the wall; 3. The *nucleus* (or cytoblast[4]), also described (p. 22); and 4. The *protoplasmic fluid*[5] (p. 20), which

---

[1] Κύτος, a cell; γένεσις, origin.

[2] Quekett's Lectures on Histology, 18.

[3] In German, *Primordial-Schlauch*—the *utricle protoplasmique* of Trecul.

[4] Κύτος, a cell; βλαστὸς, a germ.

[5] Πρῶτος, first; and πλάσμα, formative matter: *Cytoblastema* (κὺτος, a cell; and βλάστημα, a germ) of Schleiden and others.

fills the space between the nucleus and the cell-wall, and contains an abundance of small granules floating in it. "As the cell enlarges by the growth and expansion of its walls, the space between the latter and the nucleus becomes filled with watery sap, leaving the protoplasm merely as a viscid coating of the inside of the primordial utricle, and of the nucleus, if this remains." The primordial utricle appears to have the same chemical composition as the protoplasm, and may be regarded simply as this substance, which has acquired the consistence of a soft membrane. Protoplasm contains nitrogen in considerable quantity, in addition to the carbon, hydrogen, and oxygen found in the cellulose of the cell-wall. It is coloured yellow by iodine, and coagulated by alcohol and acids. The substance of which it principally consists is *Proteine*, which, under the various forms of diastase, gluten, fibrine, vegetable albumen, &c., is widely diffused in the vegetable kingdom.

Original Cell-Formation.—As far as we are able to learn, every cell originates "within another cell, or in a fluid which has been contained in and elaborated by cells." This is known, in contradistinction to the opposite or exogenous doctrine,[1] as the "endogenous" or "intracellular" theory of cytogenesis.

A portion of the protoplasmic fluid accumulates near the centre, forming a solid or semi-solid globular or ovoid mass; and another and thicker layer (the *primordial utricle)* forms on the outside of this, giving the mass a regular outline. The cellulose *cell-wall* is subsequently deposited, and the outline of the cell formed. The nuclei, of which one or more may be present and develop into new cells, are very minute, especially when several are present, in comparison with the parent cell.[2]

In some of the lower Algæ there is a variation on this. In these plants a considerable portion of the contents of a cell condenses into a round mass, the surface becomes coated with a layer of

---

[1] Of late years Mirbel's notion that cells could originate in the protoplasmic fluid, somewhat like the vacuoles in a loaf of bread, has been adopted by Mr Wenham (Trans. of the Mic. Soc., n. s., iv. (1856) 1-60), with the support of Dr Carpenter, who considers that the observations made by that gentleman "afford strong reason for the belief that in some cases at any rate the leaf originates in a layer of protoplasm, which is in the first instance homogeneous, but in which large vacuoles become the cavities of the first cells, whilst the plasma between them, acquiring increased consistence, is converted into the walls of these cells. Sometimes, when one of the first-formed vacuoles is unusually large, it is divided into two by the extension of a bridge of protoplasm over it. On the other hand, if the plasmatic division between the vacuoles should be unusually broad, a new vacuole forms in its substance, and there is formed a congeries of cells having a certain average size and shape, which, when matured, begin to multiply by self-division, and gradually evolve themselves into the perfect leaf."

[2] See the original memoir of Schleiden on Cytogenesis, translated in Ann. des Sc. Nat., xii. 242.

protoplasm or primordial utricle, and this, in its turn, with a membrane of cellulose, thus completing the cell. In *Vaucheria* the whole of the green contents at the end of certain branches condenses into a globular mass, which, becoming coated with a cell-membrane, is generated into a cell. In *Zygnema* the whole contents of two cells unite and form a single new cell after a similar fashion. "In the higher or flower-bearing division of plants, this process of original or *free* cell-formation occurs only in the sac in which the embryo is formed. The first cell of the embryo originates in this way, but all subsequent growth is effected by a different process. In the simplest grade of plants it occurs more frequently, but only in the formation of those bodies which in them take the place and fulfil the offices of seed—that is to say, which serve for reproduction."

As the cell-wall increases much faster than the nucleus, this latter portion soon disappears, or remains united in traces to the wall of the cell, although in old cells even the primordial utricle and protoplasm disappear, and only the cell-wall remains. In this case, the cell may be said to be *dead.* When the vitality of a cell is gone, the interior gets filled with air instead of fluid, as witness the pith of a plant after a few years' growth, which is white, light, and dry compared with the greenish colour it shows in the first year of the growth of the plant, at which period the cells composing it are filled with sap. But the *plant* increases, not by original cell-formation, but by

Cell-Multiplication. — Every cell has the power of dividing itself into two, each of these again into two, and so on, multiplying with great rapidity. In this way the embyro is formed from the original cell, of which all plants at one time consist—the seedling from it—and from the seedling the herb, tree, or shrub; in a word, the plant grows by cell-multiplication.

This is called *merismatic multiplication*, and is accomplished in this manner: The cell (which generally soon attains its full growth) has, as we have seen, in its interior, a nucleus; this nucleus divides in two: then the cell-wall and the primordial utricle fold in on either side and form a partition, with half of the divided nucleus in each division; and finally, a layer of cellulose is deposited as a permanent wall, and the process of cell-multiplication is complete.[1]

In this manner, by the multiplication of cells and the union of cells thus multiplied, cellular tissue or parenchyma is formed. In some of the simplest plants, the cells separate as they form, and become independent; and Asa Gray has described the following

---

[1] This doctrine of Mohl has been combated by Pringsheim (Untersuchungen über der Bau und Bildung der Pflanzenzelle, 1854), but without, we believe, shaking its main foundations.

variation as occurring in a species of *Palmella* very common in shallow fresh water, where it forms green slimy masses in early spring: At each step of the multiplication described, new cell-walls are formed, and the old one—for instance, that which covers the cell before being divided—forms a part of the thickness of the coat of each, or is destroyed by the distention, or else is dissolved into jelly. He also describes a slight modification of this as occurring in

Free multiplication within a mother cell.—This is intermediate between the original cell-formation and ordinary cell-multiplication. "Here the whole contents of a living cell, by constriction or infolding of the primordial utricle, divide into two or four parts; and these may be again divided: each portion has a coat of cellulose deposited over its surface, and thus so many separate cells are produced, lying loose in the cavity of the mother cell, whose thin and now dead cellulose wall, which is all that is left of it, usually disappears sooner or later, or is broken up by the growth of the new crop within." In this way are formed the grains of pollen in the anther, and the spores, or bodies which answer to seeds, in the higher grades of flowerless plants.

Growth of cells.—By appropriating assimilatory matter, the young cell increases in size, and grows—the boundaries, as well as the thickness of the cell-walls, increasing. If free, it will keep a globular form; and if pressed on by its neighbours, it will assume the various shapes we have already described (p. 9). If it increases more in one direction than another, it becomes oblong or cylindrical, and may even in this way be drawn out into a slender tube, as in fibres of cotton. In some of the simpler plants cells continue to increase by *gemmation*, or budding in one direction without a corresponding increase in any other, so that the plant is a *moniliform* thread; or sometimes a new point of growth commences on the sides of a cell, giving rise to *branched cells* (p. 12).

The transference of fluid from cell to cell takes place by means of *endosmose*[1] and *exosmose*[2]—two terms applied by Dutrochet[3] to the phenomenon of two fluids of unequal density, when separated by an organic membrane or by any thin and porous partition, passing from the one compartment to the other more or less rapidly, "according to the thinness of the intervening partition and the difference in the density of the fluid in the two sides—a small quantity

---

[1] Ἔνδον, within; μάω, I seek.

[2] Ἔξω, outwards.

[3] Mém. pour servir à l'hist. des végét., i. 1-99. Of late it has been proposed to replace Dutrochet's terms by *Osmose* and *Diosmose*, and by Schumacher (Die Diffusion in ihren Beziehungen zur Pflanze, 1861) to use the word *membranous diffusion* (Membrandiffusion). Dutrochet himself latterly used also the word *endosmose*, modified by the adjectives *implétive* and *déplétive*, according as the entrance or exit of liquid was referred to. (Article "Endosmosis," Cyc. Anat. and Phys., ii.)

of the denser fluid passing into the lighter, but a much larger portion of the lighter passing into the denser ; and this continues until the two fluids are brought to the same density." In this manner sap will pass, independently of the vessels, from the roots into every leaf and branch through what might seem impervious membranes, and from cell to cell, as can be easily seen when a cellular body swells out if immersed in water—*e.g.*, a dried seaweed, which is a plant altogether composed of cells. The communication of fluid from cell to cell can be still better demonstrated if a drop of coloured fluid (such as a solution of iodine) is allowed to fall on a thin slice of cellular tissue (such as that from the potato) under the field of the microscope. Endosmose, however, though a physical operation, and one which can be imitated outside the organism by the aid of a bladder full of water placed in a vessel of syrup, will not *entirely* explain the absorption of fluids by the radicals or their transmission from cell to cell, which is a vital act impossible to imitate in all its phases.

CHAPTER II.

WOODY AND VASCULAR TISSUES.

FROM the ordinary cellular tissue up to that known as *Prosenchyma*[1]—a general term applied to the tissues "*formed of elongated cells, especially those with pointed or oblique extremities,*"—there is every form of gradation. One of the most characteristic forms of this *prosenchyma* is that known as *woody* or *ligneous tissue* or woody fibre[2]—the latter term being applied to it by the older botanists, under the belief that it was a tissue, distinct, *per se*, from cellular tissue. The term is still convenient; but the younger student, by whom it is frequently used, especially at the commencement of his botanical studies, ought to remember that *woody fibre, and all the other tissues, are only modifications of the primary cell.*

Fig. 22.—Group of fusiform wood-cells, constituting woody tissue or pleurenchyma.

It makes up a large portion of the tissues of trees, shrubs, and herbaceous plants, but is wanting in mosses, sea-weeds, lichens, and fungi; though in these, especially in the two latter orders, a fibrilliform or interlaced tissue, composed of much-elongated tube-like cells, appears to take its place.[3] In woody plants there are other tissues in addition, which help to build up the structure.

"Forming wood" consists of long prismatic, nearly square or oblique-ended cells, which, as the young cells lengthen, become more oblique, until finally they overlap each other in the form of a splice, to form the ordinary familiar woody tissue. The wood-cells vary in size in different species; those in the linden are about $\frac{1}{1500}$, and those of the pine about $\frac{1}{250}$ of an inch in diameter; but they are usually much smaller

---

[1] Πρὸς, close to.

[2] *Pleurenchyma* (πλευρά, a rib) of Meyen; *vaisseaux imparfaits*, or *cellules conductrices* of Duchartre; see also Caspary, Uber die Gefässbündel, in Monatsber. der Akad., Berlin, 1862.

[3] The *dædalenchyma* (δαίδαλος, entangled) of some authors. In lichens it is harder and firmer than in the other orders named.

than parenchyma, especially in herbaceous plants (Gray). The density or compactness of wood depends on the thickness of the cells and their compact arrangement in threads or masses, which are arranged through the stem of the plant. In old wood, such as the heart-wood of trees, the walls often get so thickened that the cell becomes almost solid.

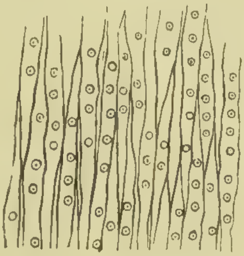


Fig. 23.—Shaving of wood from a fir, showing the prosenchyma with disciform markings always found on the wood-cells of Coniferæ.

Punctations.—The thickening is generally so uniform that, with the exception of the discs described (p. 18), there are no markings on the wood-cells.[1] These discs are arranged in regular perpendicular single, double, or triple rows, according to the species of plant. At one time it was believed that this dotted tissue was peculiar to the *Coniferæ* (firs, pines, cypresses) and *Cycadaceæ;* but we now know that this idea, which has led and is yet leading to much error in palæontology, is erroneous.[2] No doubt in the Coniferæ these disc-marked wood-cells make up the wood without any admixture of ducts, and have been therefore believed to be a form of vascular tissue. They occur, at least, also in the "star anise" (*Illicium floridanum*) of the Southern United States; and they are known to be present in several other dicotyledonous trees. In the wood of the Winter Bark genus (*Drymis*), the tissue shows dots and transverse marks mixed up together. Just as we find a transition from cellular tissue to woody tissue, so also do we find a transition from it to vascular tissue in the case (*e.g.*) of the yew, where the discs are few, and in the cells of which delicate spiral markings appear. In this case the deposit which formed the discs and that which formed the spiral must have been dissimilar. In *Oncidium altissimum*, Lindley describes a spiral inside the wood-cells. A spiral is also seen in the wood-cells of the lime tree.

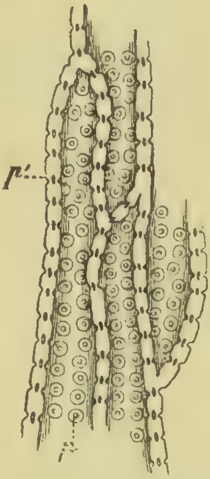


Fig. 24.—Longitudinal section of wood-cells, showing areolar punctations, discs, or "maculæ" (Schacht). *p* Front view of the punctations; *p'* Profile view, as seen in a longitudinal section of the walls of the cells.

When two disc-marked wood-cells are coherent, the discs of the two cells lie exactly opposite to each other, so that in very thick-walled cells the cavities of the two cells are only separated from each other in the canals of the pits—the primary walls of the

---

[1] Disc-bearing woody tissue; Glandular wood-tissue of different authors.

[2] This was first pointed out by Mohl—Ann. des Sc. Nat., 2d ser., xviii. 321.

coherent cells forming a thin partition. Sometimes the discs are drawn out so as to appear as short slits; at other times they are not scattered irregularly, as in the above case, but are arranged in a spiral direction, and correspond in position but no longer in form, since, being situated obliquely on opposite sides of the cell, they cross, and only correspond at their central part.[1] This form, which causes the discs to appear like minute St Andrew's crosses surrounded by a ring, is well seen in *Gingko biloba*, a conifer. Principal Dawson has also figured it in certain fossil plants of Devonian age; and Mr C. W. Peach has obtained fragments of plants from the "Camstane Quarry" (Carboniferous) in Arthur's Seat, near Edinburgh, which also show this structure.

Bast-tissue is the woody tissue of the bark, and is found in the liber or inner layer of the bark. The cells composing it usually consist of, or contain "much longer, very thick-sided, and tougher but more soft and flexible cells than those of the wood itself," thus giving the bast-cells that flexibility and strength which render them so valuable as fibres for the manufacture of cloth and cordage. Mohl[2] says that there are few plants in which they are more than $\frac{1}{12}$ of an inch in length; though in the American leatherwood (*Dirca palustris*)—so called from the great toughness of its bark, owing to the presence of these cells—they are $\frac{1}{6}$ of an inch in length, with an average diameter of only $\frac{1}{2000}$ of an inch. In the flax[3] and milkweeds (*Asclepias*) they are an inch long; and in the nettle, which yields a good fibre, longer still.

To recapitulate: Woody tissue embraces the following modifications: 1st, *Simple woody tissue*, in which the walls of the cells may be perfectly unmarked, though of a considerable thickness, as in the ordinary tissue of wood and in bast-cells; 2d, In which both dotted and transverse markings are found together on the cells (*Drymis*)—thus combining the character of both the transversely barred and dotted cells already described (p. 18); 3d, In which a thin spiral appears, as in *Oncidium altissimum;* 4th, When, as in the yew, there is disced tissue combined with a spiral; 5th, The true disced tissue of the Coniferæ, &c.

---

[1] Mohl, Veg. Cell, 17.

[2] Bot. Zeit., 1855, s. 876.

[3] Cotton and flax, though so familiarly classed together as textile materials, are botanically entirely different. Cotton is the long hair-like cells from the cotton-seed (*Gossypium*). These cells are tubular, and when drying flatten out, and then twist spirally; while flax is, as we have seen, derived from the liber of *Linum usitatissimum*, &c., and appears under the microscope with a plain outline. By this means the presence of one or other fibre in a fabric can be instantly detected. For instance, by this test the cloth wrapped round the Egyptian mummies was shown to be linen, and that around the Peruvian ones to be cotton.

VASCULAR TISSUE.[1]

We have seen in the preceding pages the cell either performing all the functions of the plant, or multiplying to form *cellular tissue*—a mass of united cells; or, secondly, these cells may elongate, and, with their cell-walls thickened by internal deposits, form *woody tissue.* In neither of these cases are there any true conducting vessels formed. We now come to the last modification of cells,—viz., that in which they form vessels by being placed end to end, and the transverse partitions getting absorbed—just as a number of casks, if placed end to end, one above another, would form hollow cylinders if the contiguous tops and bottoms fell out.

It must therefore follow, if this is the mode in which vessels are formed from cells, that these vessels, as in the woody tissue, must partake of all the characteristics of the individual cells of which they are composed. Tubes or vessels are consequently divided, according to the markings on the cells of which they are composed, into—1. Simple-walled or laticiferous vessels; 2. Tracheary vessels; 3. Punctated and barred vessels. These three great divisions have some minor modifications, which we shall consider under the different headings mentioned.

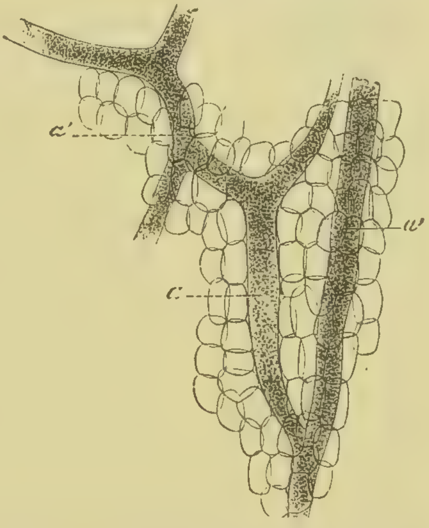


Fig. 25.—Fragment of a laticiferous vessel from the cultivated fig (*Ficus carica*, L.) The globules of latex can be seen, owing to its transparency. The vessels in the figure appear wider (a) or narrower (a' a') at certain points, owing to the knife, in making the section, having let out some of the globules.

Laticiferous or Simple-walled Vessels.[2]—These remarkable vessels were first fully called attention to in 1836 by C. H. Schultz of Berlin,[3] and were again the subject of elaborate memoirs by Dippel and Hanstein in 1863. Nevertheless, their nature, contents,

---

[1] *Angienchyma* (ἄγγος, a vessel). The words "duct" and "vessel" are generally used synonymously, though attempts have been made to reserve the former name for vessels proper, the latter for wood-cells.

[2] *Lebenssaftgefæsse* (vessels of the vital sap), *Milchsaftgefæsse* (vessels of the milky sap), *vaisseaux propres* (proper vessels), &c., of various German and French authors; the *Cinenchyma* (κίνεω, I move—from the movements of the latex under them) of Morren.

[3] Die Natur der lebenden Pflanze (1823-28); Sur la circulation et sur les vaisseaux laticifères dans les Plantes (1839); Die Cyclose des Lebenssaftes (1841).

and uses are far from being thoroughly known. The following facts in regard to them may, however, be accepted by the student as resting on a tolerably sure foundation.

Their walls are generally thin, deprived of any markings; more or less winding in their course through the tissues, unequal in their diameter at different points; and, above all, they are frequently branched, different tubes anastamosing to form a sort of open network in the tissue. Minor characteristics may be noted in that they are opaque-walled, and in that their contents are opaque, white, or coloured. In shape they are more or less cylindrical when they are isolated, and prismatic or angular when they are united, on account of the mutual pressure which they exert on one another. Their average diameter is about $\frac{1}{1400}$ of an inch. They exist in most dicotyledonous and monocotyledonous plants, and Schultz has even found them in some acotyledonous orders. In these divisions they, however, occupy different places. In Dicotyledons and Monocotyledons they are constantly found in the vascular bundles of the leaves which are known as *nerves*. In the stem of Dicotyledons they are seen in the bark; in other instances they are found in the pith. In the stem of Monocotyledons, on the contrary, they are found in each of the woody bundles scattered through the cellular tissue of the stem. In some plants—*e. g.*, the hedge-maple—they are confined to the young shoots.


Fig. 26.—Globules of latex from *Ficus carica*, L., much magnified.

Regarding the origin of the laticiferous vessels, the student ought to know that though they are generally believed to be formed like other vessels, by the union of lines of cells, this opinion is not universally held by botanists. On the contrary, it is stoutly maintained by some physiologists of great eminence that they are simply intercellular canals, enlarged by the accumulation of the *latex* (p. 43) in their cavity, and around which the liquid secreted forms little by little, by a simple deposition, the walls of the canal. This latter opinion is adopted by Mohl, Schleiden, and others; while for the former, which is more generally adopted, the names of Unger,[1] Schacht,[2] Dippel and Hanstein,[3] Vogel, Trecul, &c., stand sponsors. Unger, indeed, describes and figures the laticiferous vessels in the root and stem of *Chelidonium majus* (common celandine) as formed of cells easily distinguished the one from the other; and Schacht, in terms equally explicit, describes them as formed of several cells fused into one.[4]

---

[1] Grund. der Anat. u. Phys. der Gewächse, s. 159.

[2] Die Milchsaftgefässe d. Carica, 1857.

[3] Comptes rendus, lx. (1865) 78, 522.

[4] The truth probably is, that in some cases they are simply intercellular

Laticiferous vessels may be divided into two categories: (1.) Those in which the tubes branch but do not unite with the neighbouring tubes, and accordingly form no network, and are all, in all stages of their growth, inclined to be semi-articulated—*i.e.*, composed of cells which, on maceration, separate easily (Ex. *Chelidonium majus*, *Euphorbias*, *Vinca minor*, Chicory, &c.); and (2.) Those in which they form a network, and show no signs of articulation.

In 1853, Th. Hartig discovered, between the liber and the cambium, elongated thin-walled cells, generally cylindrical, superimposed in rows, and remarkable in so far that they present either on the diaphragm formed by their superposition, or upon their lateral walls, minute punctations, so that they resemble little sieves. Hence they were called *cribriform tubes*.[1] It has been supposed by some that these are the cells which unite to form the laticiferous vessels, and it is pointed out that they replace in milky-juiced plants those sieve-like cells which are found in the liber of other flowering plants.

Latex.—We now come to speak of the *latex* or milky juice found in the interior of these vessels. This and the containing vessels are found in a great number of plants familiarly known as possessing milky juices, such as the spurges (*Euphorbia*), figs, dandelion, lettuce, &c. This juice is generally opaque, white, or more rarely coloured: for instance, in *Chelidonium majus* it is yellow, orange in the artichoke, greenish in the periwinkle (*Vinca minor*), &c. It is generally found disseminated in greater or less quantities through every organ of the plants in which it is found. *Microscopically* (fig. 26), the latex is shown to be formed of an enormous quantity of very minute globules floating in a liquid to which they give the opacity or coloration: it is generally bitter and acrid in taste. *Chemically*, we find that this latex contains materials which give many plants in which it is found a high commercial value—caoutchouc and analogous materials being forms of it.

For example, caoutchouc or India-rubber is derived from various species of trees—viz., *Ficus elastica* and *Castilloa elastica* of the order Artocarpeaceæ, and *Urceola elastica*, belonging to the Apocynaceæ. The India-rubber of Brazil is furnished by *Siphonia brasiliensis*, and that of Guiana by *Hewæa guyanensis*, both

---

canals, as may be seen in *Alisma Plantago*, and other monocotyledons; as also in *Rhus*, wild angelica, and the Umbelliferæ generally, and, according to W. R. M'Nab, in the young stem of the ivy (Trans. Bot. Soc., ix. 316). These canals are different from the resin canals of the Coniferæ in wanting the delicate lining.

[1] *Siebrœhren* in German. Mohl, in 1855, called them *Gitterzellen*, or *cellulæ clathratæ* (Bot. Zeit., 1855, §§ 873, 889). He has also called them, as found in the isolated vascular bundles of the monocotyledons, *vasa propria*; in French, *cellules treiblisées*, or *grillagées*, &c.

Euphorbacious trees. One of the Sapotaceæ (*Isonandra gutta*) of the Malay Islands furnishes in its latex the familiar *gutta-percha*. The latex, again, of *Antiaris toxicaria* (Artocarpeaceæ), furnishes the celebrated poison of the Javanese, known as *Upas antiar*, and the origin of the fabled "upas-tree" invented by the "Puck of commentators," George Steevens, and perpetuated by Erasmus Darwin. Karsten, however, found that when standing under one of these milky-juiced trees in Brazil, for the purpose of collecting some of the latex, his skin got seriously blistered, owing to the poisonous emanation from the fluid. It may be also noted that several species of *Rhus* found in America (*R. toxicodendron*, &c.) are popularly known as "poison oaks," from their blistering the skin coming in contact with their foliage. It is said that so sensitive are some people to the poison, that they will be affected by the smoke from a fire composed of these bushes blowing over them.[1]

By contrast, some other trees of the same order, *Galactodendron utile* and *Ficus brasiliensis*, have a latex rich in sugar and albumen; and that of *Tabernæmontana utilis* or Hya—Hya of Guiana—is even used as vegetable milk; while a close ally in the same natural order, *Tanghinia venenifera*, furnishes in its latex a violent poison. *Galactodendron utile*, from the use made of its milky juice, is well known under the Spanish name of *Palo de vaca*, or cow-tree of the English.

Two opinions are held regarding the uses of the latex: one is that it plays an important part in nutrition, and is the elaborated juice after descending from the leaves; the other belief, much more generally adopted, and more in accordance with reason and facts, is that it is simply a material secreted by the living plant, and plays but a feeble part in nutrition. Schultz, Schleiden, and others, described a regular circulation ("cyclosis") of the latex in various plants; but of late, Amici, Treviranus, Dutrochet, and Mohl,[2] have denied the existence of this—asserting that if any such movement exists, it is merely mechanical from one part to another when the plant is injured, and the juice is allowed to escape. We are, however, of opinion that these eminent microscopists are wrong, and that the prior view is the correct one. If the under side of the leaf of *Chelidonium majus*, *Taraxicum*

---

[1] R. Brown (Campst.), Trans. Bot. Soc., Edin., ix. 399.

[2] Bot. Zeit., 1843, s. 563. The student, however, in weighing the argument which Mohl and Schleiden brought against Schultz's theory of the milk-sap, must take into account the violent antipathy which both, especially the late eminent Tubingen Professor, appear to have entertained to anything emanating from their scarcely less distinguished Berlin rival—an antipathy often expressed in language which, however it might be considered suitable for a botanical controversy in Germany, would, in our more westerly longitude, be deemed decidedly unparliamentary.

officinale, the bracts of the common bindweed, the lower surface of the split stipules of the India-rubber plant, or any such milky-juiced plant, is put under the microscope, and a strong reflected sunlight be thrown on it, a distinct movement can be seen—sometimes very rapid, at other times slower; and what is more curious, the direction of the circulation can be changed at will by the interception of the sunlight. It is not the result of evaporation.[1] Amici also noticed the effect of the sunlight in reversing the current in the leaves of *Tragopogon*, but believes that the motion of the sap was produced by mechanical causes.

Tracheary Vessels.[2]—Under this name we include all vessels in which the thickening on the interior of the cell-wall assumes a more or less spiral arrangement. When the thread inside is closely coiled with the different spirals firmly united together, it is almost impossible to detect any membranous tube-wall at all; and the presence of this has in these cases been even doubted, or it has been asserted that at most it did no more than simply solder the different turns of the coil together. The tube-wall membrane, however, exists in all cases, but is very thin, transparent, and very little resistant or elastic, tearing with the utmost facility. It was long believed that this spiral thread was solid; but it has been shown by the researches of Hedwig, Mustel, Link, Visiani, and lastly by Trecul,[3] that it is in reality hollow, and filled with a gelatinous material of a colour different from that of the tube-wall, and of a variable consistency. It is generally simple and undivided, but at other times becomes bifurcated in a dichotomous manner.

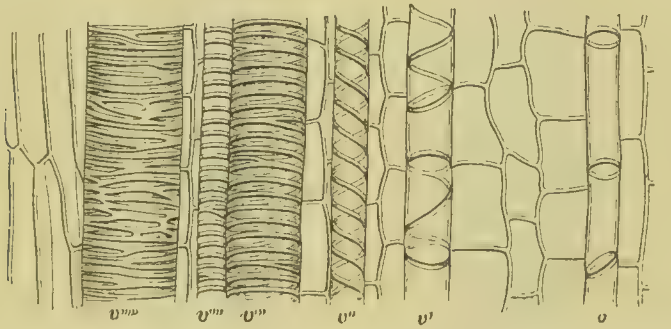


Fig. 27.—Longitudinal section of a portion of the stem of the garden balsam (*Balsamina hortensis*, Desp.) We see, 1st, An annular vessel, v; 2d, A spiro-annular vessel v'; 3d, Three tracheary or spiral vessels v'' v''' v''''; 4th, A large reticulated vessel, v'''''.

---

[1] Dr H. C. Perkins in American Naturalist, 1870, 318.

[2] *Trachenchyma* of Morren; *trachea*, the windpipe—which is, again, from τραχυς, rough—and ἐνχύω, I infuse—a barbarous union of Greek and Latin. The tissue into which it enters is also called *fibro-vascular* tissue, just as cellular tissue, composed of cells which contain a spiral in their interior, is called *fibro-cellular*.

[3] Ann. des Sc. Nat., 1854.

In this case, if we unroll each trachea, we find it composed of two, three, four, five, or often of a great number of threads, united to form a ribbon-like structure.[1] This is frequently seen in monocotyledons, particularly in the banana. In the immense majority of cases, however, the spiral thread is simple, non-bifurcating. In many plants there are two, or even three threads, each turning in an opposite course within the vessel. De Candolle counted as many as seven in the tracheary vessels of the banana, and in one vessel of the same plant La Chesnaye affirmed that he saw as many as twenty-two spirals. In diameter the spiral thread varies from $\frac{1}{2000}$ to $\frac{1}{10000}$ of an inch.

The nature of vessels is well shown by the mode of termination and commencement of these tracheæ or spiral threads. Each ends in a cone more or less elongated at its extremity, and another commences by being applied against the first by a similar termination—in such a manner that it appears to be continuous. They are rarely longer than half an inch. In the stem of dicotyledons, tracheary vessels are found surrounding the pith, and form what is known as the "medullary sheath." In monocotyledons they are found in all the wood bundles scattered through the cellular tissue which forms the mass of the trunk. They are also found in the nerves of leaves, and in the petals of the flower, which, we shall find by-and-by, are only modified leaves. Lastly, we observe them in the radicles, especially of monocotyledons. The spiral thread can be seen on breaking the leaf-stalk of almost any plant (the hyacinth, for example) and gently drawing the ends asunder, when the thread appears in the form of a fine cobweb. In the banana the threads are united in the band-like form described, and are even used in manufactures. For instance, in *Musa textilis* of Manilla these fine cobweb-like threads are extracted and largely used in the production of delicate textile fabrics.

The spiral thread is not found in all tracheary vessels in a continual coil, but is more or less broken; hence these vessels may be classified into several subdivisions, distinguished by the more or less continuous nature of this spiral thread, though there is every gradation uniting all the forms together. Instances are seen in which the spiral will commence in detached rings or tracheæ and end in a spiral.[2] Hence these have been called spiro-annular vessels. Schleiden[3] considers that the various forms of tracheary vessels are only modifications of one another—a view which is now gene-

---

[1] Which, the student will be pleased to learn, has been called by some nomenclators a *Pleiotrachea* (πλείων, more).

[2] Moldenhawer in Anat. des Plantes, i. fig. 3; Slack in Ann. des Sc. Nat., 2e sér., i. pl. 7, fig. 20, 21; and Richard, *l. c.*, 34.

[3] Ann. des Sc. Nat., 2e sér., xiii. 364.

rally adopted ; though Mohl,[1] on the contrary, maintains that they "present the same structure at every epoch of their existence." Adopting the former view, the modifications of the tracheary vessels are then as follow:—

(α) *The spiral vessel*, which we have already described as the type of the division.

(β) *The annular vessel*, in which the spiral thread seems only to form detached rings.

(γ) *The reticulated vessel*, in which it branches and anastomoses, forming a network.

Reticulated and annular vessels (sometimes called "false tracheary vessels") abound most in herbaceous plants; but in the stem of *Polygonum orientale*, and other plants, almost every form and gradation occurs. The use of the tracheary vessels is probably to convey air; though in the younger states of the plant, or during the season when the whole stem is gorged with sap, they may also assist in conveying that.

Punctated and Barred Vessels.—In this division the deposit inside the cells forming the tube takes the form of little dots or more or less perfect transverse bars—these forms, however, dovetailing into one another by numerous modifications, which show them to be only forms of one and the same organism. They have, however, received separate names, and have even been classed as

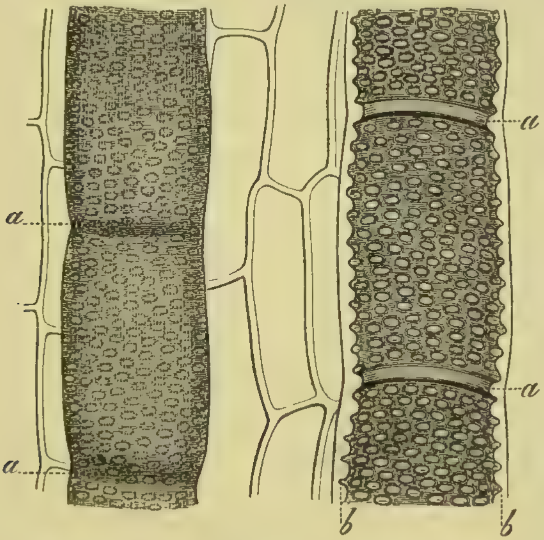


Fig. 28.—Longitudinal section of portion of the stem of *Aristolochia Sipho*, L'Hérit., in which are seen two large punctated vessels,—the one to the right entire, with constrictions, *a a*, which indicate the point of reunion of two primitive cells; the other to the left, cut longitudinally, to show its interior. *a a* Two annular markings, the remains of two horizontal divisions; *b b* A section of the walls in which punctation forms a little recess.

---

[1] Ann. des Sc. Nat., 2e sér., xix. 242.

distinct tissues; so that in order to simplify the subject, we shall arrange them as subdivisions under the names most commonly applied to them by descriptive histologists:—

(*a*) *Dotted vessels.*[1]—This is the simplest modification. Here the thickening deposit appears through the transparent wall in the form of little dots. They often exhibit constrictions, which point out their origin to be in a row of cells, placed end to end, and becoming a tube by the absorption of the partitions between them. This form of vessels Richard[2] divides into two classes, which it may be convenient to adopt. The first are *simple dotted vessels*, in which the tube is cylindrical or a little compressed, having a considerable diameter. Their walls show the punctations, generally very small, sometimes even granular, and rarely equal in size, and sometimes irregular in distribution. In general, however, these dots are disposed in perfectly horizontal lines. They are chiefly seen in the woody bundles of the stem of monocotyledons (fig. 29). They exist, however, also in the woody layers of dicotyledonous stems. The second class are the *areolar dotted vessels*, in which there is in general a circular areola surrounding the punctation like a circular cushion. This appearance is probably owing to air in the cavities between contiguous vessels. A curious fact has been observed in these dotted vessels, and that is, that they will often differ in the same part, or even in the same cell. Thus Moldenhawer observed that in a tube of *Tilia* one side was dotted, and the other had imperfectly-barred markings. Again, in Coniferæ the side of the dotted vessels facing the medullary rays shows areolar punctations, while the other side has only plain dots. In general terms, it may be affirmed that the structure of dotted vessels is affected by the tissue with which they are in contact. All the walls of vessels united with other vessels of the same nature present areolar punctations. But if the organs which touch them are of a different nature, the points in contact may show simple punctations, horizontal or oblique bars, or even spiral markings, according to the nature of the contiguous vessel.

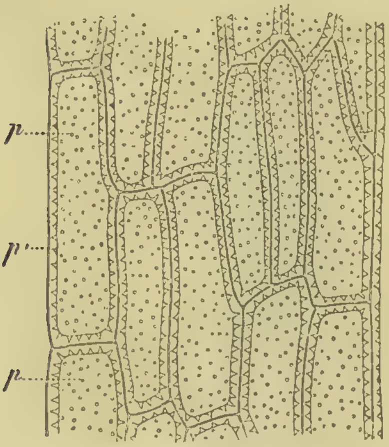


Fig. 29.—Longitudinal section of cylindrical cells, with walls moderately thickened and abundantly punctated, from *Bragantia Wallachii*, R. Br., an exotic shrub. The punctations are seen both in a front (*p p*) and in a profile (*p'*), or longitudinal sectional, view.

---

[1] *Bothrenchyma* (βοθρος, a pit) or *Taphrenchyma* (τάφρος) of Morren; pitted or vasiform tissue; porous vessels.

[2] Richard, *l. c.*, 28.

These dotted vessels are often of considerable length, and are of greater calibre than any other in the wood (in which part of the vegetable structure they chiefly abound), and accordingly they show markedly on transverse section. The "pores," conspicuous to the naked eye on the transverse sections of coarse-grained wood, like oak, chestnut, mahogany, as well as the longitudinal channel seen on longitudinal section, are these dotted vessels. In the plane they are particularly well marked.[1]

(β) *Imperfectly-barred vessels.*[2]—Here we find the markings extended transversely, or more rarely obliquely, in the form of broken bars—unequal, or almost equal, among themselves. Sometimes these markings are very linear, at other times broader and rounded at both extremities. This kind of tissue is very generally found in the wood of dicotyledonous plants, or composing part of the bundles of monocotyledonous stems. In these vessels there are often seen slight constrictions, or remains of transverse partitions, pointing to their being originally formed of superimposed cells.

(γ) *Scalariform vessels.*—From the imperfectly to the perfectly barred vessel there is a regular gradation. In this kind of tissue the vessels are usually prismatic from mutual pressure. The markings are in the form of transverse lines closely united together, but with regular and uniform distances between them, stretching nearly right across each face of the prismatic tube; hence, from their resemblance to the bars of a ladder (*scala*), they have received their distinctive name (fig. 30). This tissue is very characteristic of both the aerial and underground stems of ferns. The markings are often spiral in their arrangement, and can be unrolled, or rather torn out, in spiral ribbons, for in them the filament, instead of being only in apposition, as in the true spiral vessels, is soldered to the tube; hence such vessels are called *closed ducts*.

We have thus seen that all vessels are modifications of each other, just as the original cells out of which they were formed were all modifications of one simple cell. Though it has been necessary to arrange the different forms which they eventually take into classes, yet these classes are to a great extent artificial—the one graduating into the other. A vessel will even in different parts of its course have different characters, and be successively imperfectly barred, punctated, scalariform, reticulated, &c.; so

Fig. 30.—Portions of scalariform tissue from *Aspidium filix mas.*

---

[1] *Vaissaux rayés* of French botanists.

[2] Punctated vessels occasionally get filled up with cellular tissue. *Tyloses* is the name which has been applied to this peculiarity.

that Mirbel's class of "mixed vessels" is perfectly unnecessary and inadmissible. To sum up—we see that the different appearance which the same tube may present at different points of its course may be due to: 1st, The original structure of the cells of which it is composed, which structure may be different in each cell out of which it is made; 2d, The influence which the neighbouring tissues invariably exercise on the vessels with which they come in contact.

Vascular Bundles.—Vessels by their union form vascular bundles, often called fibres, though this name is equally applied to the woody tissue, which, in conjunction with the vascular, makes up all the parts of the plant which are not composed of cellular tissue or parenchyma. In cellular plants like fungi, algæ, lichens, and mosses, there are no true vessels; and hence these plants are composed simply of cellular tissue. When we examine a vascular plant at the earliest stage of growth, we equally find that it is entirely made up of cells. After a while the vessels appear, being formed, as we explained at the beginning of this section, by the absorption of the tops and bottoms of contiguous cells—a discovery great in its very simplicity, and for which we are indebted to Treviranus and Mirbel. In fig. 28 this is shown. In this longitudinal section of a portion of the stem of *Aristolochia Sipho*, L'Hérit., we see two great dotted vessels, the one to the right entire, with two constrictions, *a a*, which indicate two points of union of two primitive cells; the other to the left, with the interior exposed in order to show at *a a* two annular pads, remains of the two horizontal partitions; at *b b*, the section of its walls shows each punctation, as a sort of little recess. Vessels are generally of great length, but it is very difficult to follow them up; so that on this point our information is as yet somewhat imperfect.

Transitory vessels.—In general, vessels when once formed remain during the life of the plant. Before, however, dismissing the subject, a curious exception to the rule ought to be noticed. In certain aquatic plants, generally supposed to be entirely cellular in their structure, Robert Caspary of Königsberg discovered that in early life they possessed a tracheary vessel, which in the process of growth gets absorbed, leaving only a longitudinal canal.

The cells and vessels are united together by the intercellular substance to form the body of the plant. We now come to consider the organs which these in combination form; but first we must describe a structure which is common to all the organs, besides being the simplest modification of the parenchyma—viz., the general integument or *Epidermis*.

CHAPTER III.

EPIDERMIS AND APPENDAGES.

The Epidermis[1] is a thin, transparent, but firm cellular membrane covering all the parts of the plant exposed to the action of the atmospheric air (except the stigma), and is not, as frequently described, formed of the superficial layer of the cells of the part which it covers, but is a distinct structure, composed of two parts: (1.) The *cuticle*, a thin homogeneous external part, without any appearance of organisation; and (2.) The *derma*, a more interior cellular structure. These two membranes are placed one over the other, and intimately united together (fig. 31). They are pierced by a great number of little openings called *stomata*. The appendages of the epidermis are *hairs*, *scales*, and their modifications, *glands* and *lenticels*, each of which structures we shall consider somewhat more in detail.

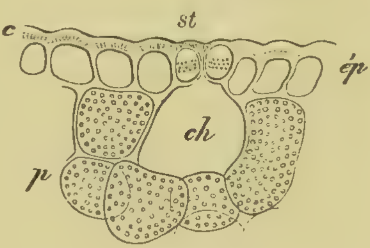


Fig. 31.—Longitudinal section of a fragment of the leaf of a hyacinth, passing through the middle of a stoma, *st*; *c* Section of the *cuticle* of the epidermis; *ép* The *derma*, the cells of which surround the stoma; *ch* The air-chamber, situated beneath the stoma; *p* Interior parenchyma of the leaf, in which the cells are filled with chlorophyll-grains.

Cuticle.[2]—It exists on the epidermis of leaves as well as on that of the stem, and, as proved by the researches of Bénédict de Saussure, Hedwig, and particularly of Brongniart, is a structure quite distinct from the layer on which it is superimposed. It exists alone on the parts of plants which are completely immersed in water (*Potamogetons*, for example). In these plants the cellular *derma* is entirely wanting. In ordinary terrestrial plants it can be peeled off by maceration in water. Its existence can also be demonstrated by a chemical test. If we treat a transverse section of the epidermis with iodine, the cellular derma will

---

[1] ʼΕπὶ, upon; and δέρμα, skin. I prefer to retain the term epidermis for the general integument as a whole, and the terms cuticle and derma for its component parts, confusion arising from using the same term (epidermis) in a general and in a special sense, as is often done.

[2] Superficial pellicle.

remain colourless, while the cuticle will turn to a deep yellow, or even brown colour. If the section of epidermis thus treated is placed in sulphuric acid, the derma, which has remained uncoloured, dissolves, and takes in most cases a beautiful indigo hue; while the cuticle keeps its yellow colour, and is not affected by the acid. The cuticle is one of the most constant parts of plants, existing on all organs and in all stages of their growth; so that it cannot be, as Treviranus and others thought, a mere secretion deposited by the epidermal cells. Moreover, it has a different chemical composition from the rest of the epidermis, being represented, according to Garreau,[1] who obtained, by a very delicate process, enough for analysis, by the formula $C_{17}H_{32}O_5$ — a formula analogous to that of caoutchouc; while the derma is represented by $C_{24}H_{40}O_{10}$. It has no appreciable organisation, though Brongniart[2] sometimes recognised the existence of granulations, disposed in parallel and spiral series; or now and then, according to Mohl, in branching lines. These facts are true of a vast number of plants. However, it ought to be noted that, in fungi, lichens, and algæ, there is no true epidermis, the tissues being all composed of the same kind of cells. Schacht has observed that in some plants the cuticle even is wanting. For instance, he found none on any of the orchids which he examined. On the other hand, on the leaves of *Cycas revoluta* the cuticle forms a thick layer. Barthélmy[3] considers that, in the interchange of gaseous molecules between the plant and the atmosphere, the oxygen and carbonic acid pass especially through the cuticle, while the nitrogen makes a way for itself through the stomata.

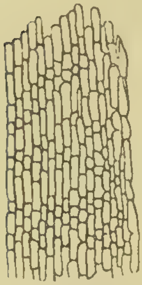


Fig. 32.—View of the tabular cells of the epidermis.

Derma.—This is the cellular portion of the epidermis underlying and united with the cuticle. It is composed of one layer of cells in thick-leaved plants, or of two, three, or four layers lying one over the other. The cells composing this layer are firmly united together; and when the firm attachment of this layer to the cuticle above is added, a considerable strength is given to the whole epidermis. Nearly always flattened in shape, the cells of the derma differ widely in form from those of the rest of the tissues lying immediately under it. When the plant on which the epidermis exists spreads out laterally, the outline of the cells is generally wavy and irregular;[4] but if it increases more in length than breadth, these are regular and elongated, and generally in longitudinal lines. The cells of the epidermis are generally without chlorophyll, though now and then instances occur in

---

[1] Comptes rendus, xxxi. (Sept. 2, 1830). [2] Ann. des Sc. Nat., Feb. 1834.
[3] Ibid., 5^e. sér., ix. 287. [4] Forming Morren's *Colpenchyma* (κόλπος, a fold).

which a few grains of that substance can be seen. The walls of the cells are usually somewhat thick, though in most cases simple, and instances are not wanting in which transparent punctations are seen.

The epidermis often contains, as we shall have occasion to notice in another place, a considerable quantity of silex, which substance impregnates the cells of the structure.

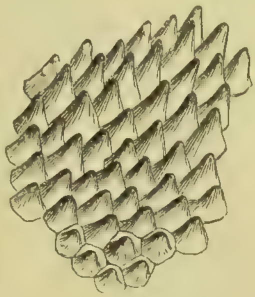


Fig. 33.—Fragment of the epidermis of a petal of a pansy, magnified to show the papilla upon it.

On the inside of the epidermis are seen a number of lines forming an irregular network, or meshes almost equal, which Hedwig, Kieser, Amici, and others, have considered as, and called the *cuticular vessels.* On the epidermis of flowers are a number of papillæ, which assist in giving the velvety appearance to certain flowers. Schleiden considered that he could see certain modifications in the structure of the epidermis on different parts which would allow it being divided into—1. *Epithelium*, 2. *Epiblema*, and 3. True *Epidermis.* But this subdivision is generally acknowledged by the best microscopists to be unnecessary.

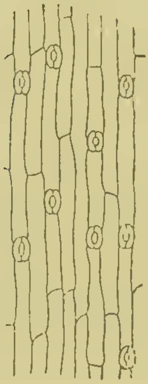


Fig. 34.—Epidermis from the hyacinth-leaf (*Hyacinthus orientalis*, L.), showing the cells of the epidermis with a rectangular, straight, and elongated contour. The stomata are arranged in longitudinal rows.

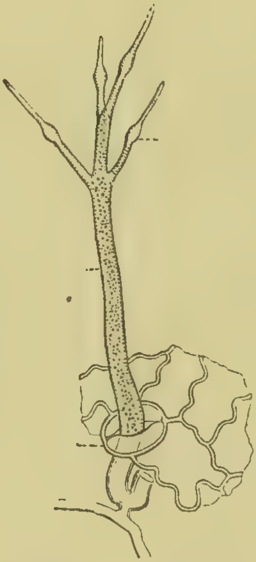


Fig. 35. — *Peronospora infestans*, Casp., a fungus sending its mycelium into the parenchyma of a potato-leaf through one of the stomata (after De Barry).

Stomata.[1]—These openings pierce the epidermis in great numbers. They are in general formed by two crescent-shaped cells,[2] united at their extremities, and forming between them a longitudinal opening or mouth (*ostiole*), surrounded by two lips, somewhat like the two sides and centre of the letter O (fig. 36). They communicate with the intercellular passage of the infrajacent tissues, and assist in the transpiration and respiration of the plant. They are found on leaves, principally on their inferior aspect, on herbaceous stems, bracts, calyx, &c., and are ordinarily wanting on roots, submerged leaves, non-foliaceous petioles, petals in general, the epidermis of old stems, that of fleshy fruits, seeds, &c. There are, however, exceptions to this rule, as the student can discover for himself by examining the epidermis of the berry of the common holly. A curious form of stoma may also be seen in the epidermis of a gourd. Some leaves have them only on one side (*e.g.*, pear-tree, olive, syringa, &c., which have them only on their inferior surface), while the greater number have them on both sides, though the inferior surface is the part on which the greatest number are found. Their arrangement on the surface of leaves is due in all cases to the arrangement and form of the cells which compose the epidermis. In those cases in which these cells are irregular, the stomata are scattered over the surface without order; but when the contrary is the case, and the cells of the epidermis are disposed in an almost equal series, the stomata are arranged regularly. This latter disposition is more often seen in Dicotyledons than in Monocotyledons. On the acicular leaves of pines and other Coniferæ, they are arranged in lines. On some plants (*e. g.*, *Saxifraga sarmentosa*), the cells among which the stomata occur are very small, are arranged in clusters, and surrounded by the larger ordinary cells of the epidermis. In the

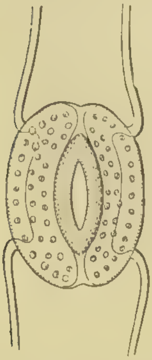


Fig. 36.—A stoma from the leaf of a hyacinth, with part of the cells which surround it—seen from above.

---

[1] Στομα, a mouth—so named by Link in 1819. He makes the plural *stomatia*, though nowadays most authors write *stomata*. They are the *spaltöffnungen* of German botanists. Before their exact use was known, various names, in accordance with the theoretical ideas of the authors of these names, were given to them—*e. g.*, *Miliary glands* (Guetard), *Epidermöidal glands* (Lamétherie), *Cortical glands* (Saussure), *Evaporating pores* (Hedwig), *Elongated* or *Great Pores* (Mirbel), *Cortical Pores* (De Candolle). As late as 1837-39, Meyen called them *Hautdrüsen*, or epidermal glands.

[2] Sometimes two, three, four (*Yucca*), or even more; or the cells may be united in a continuous margin. In the liverwort (*Marchantia*), the stoma is most complicated, being built of a tier of rings each composed of four or five cells.—(Carpenter's Microscope, § 23). The stomata of *Ancima fraxinofolia* are also curiously modified.

Nerium Oleander (rose laurel), and various species of *Dryandra* and *Banksia*, there is a remarkable arrangement of the stomata. On the under surface of the leaf are a great number of cavities, each with a straight opening, lined by long hairs. At the bottom of these cavities the stomata, which are very small, exist in great numbers. Stomata are also either found solitary or in united groups. They are usually *developed* in a cell of the epidermis by the formation of a partition, which, splitting in two, constitutes the two sides of the opening.[1]

We have already noted, in general terms, where the stomata are absent or present. Schleiden and Fournier have found them in the cavity of that part of the flower which afterwards becomes the fruit, in at least the orders *Cruciforæ* and *Passifloræ*, the latter author observing them also in *Reseda* (mignonette). The general law that they are not found on those parts of plants which are buried in the earth or float in water has one or two exceptions. They exist, according to Duchartre, on the inferior surface of the leaves of *Hydrocharis Morsus-ranæ*, L., and in considerably greater numbers on those of *Limnocharis Humboldtii*, Rich.,[2] two water-plants; and they are also found on the scale-like leaves of *Lathræa clandestina*, L., a singular subterranean parasite.

That submerged plants should want stomata is natural, and suited to their mode of existence; but still it must be noted that when a plant such as Hyacinth, which has stomata, is compelled for a number of years to develop its leaves in water, this change of habit has no effect on either the epidermis or its stomata. They are only found on the upper surface of floating plants (*e.g.*, *Nymphæa*, *Marsilea*, *Nuphar*, &c.); but on the upper surface of the leaves of these plants they are about three times as many in number as on the upper surface of aerial leaves. In some cases the opening of the stoma is surrounded by a raised border (*Proteaceæ* and *Cycadaceæ*), though in other cases the opening is below the level of the surface of the epidermis (*Gasteria*, *Aloe*, *Phormium* &c.) In *Himantoglossum* and *Helleborus* the stoma is exactly on a level with the surface.

Schacht found that the stomata of all the plants studied by him (*Aloe*, *Phormium*, *Ruscus*, *Dipsacus*, *Arbutus*, *Ilex*, &c.) were coloured, by the action of iodine and sulphuric acid, of a violet or blue colour; so that the two cells which form the stoma must always be composed of cellulose.

The number of the stomata on the leaves of different plants varies greatly, from only a few up to 160,000 on a square inch;

---

[1] Mohl in Ann. des Sc. Nat., xix. 201; Weiss in Verhand des Zoolog-bot. Vereins in Wien., 1857, &c.

[2] The leaves, however, of these plants are not really floating, but more or less upright.

or 708,750 on an entire leaf of the lilac, and 1,053,000 on an entire leaf of the lime-tree. The subject has been investigated with patient labour by the two Krokers, Thompson, Lindley, Unger, and, above all, by Edouard Morren [1] and Duchartre,[2] the result of whose researches may be summed up as follows: 1. With a few exceptions, woody plants are richer in stomata than herbaceous plants. 2. Among trees and shrubs it is on those having leathery leaves that the greatest number is found. 3. Fleshy leaves have fewest. 4. Those which have few or none on their upper surface, have them more numerous on the inferior surface than those which are not so deprived. 5. Among plants which have stomata both on the upper and under surface of the leaves, some have more on the upper than the under side, and others have an equal number on both aspects of the leaf. 6. They are fewer on those plants which are exposed to the sun than on others belonging to damp and shaded situations. 7. In general, the stomata are smaller in size when they are found in less numbers. It ought also to be noted that the greater or less vigour of the plant, and, above all, the different ages of the leaves, will modify these generalisations. The following table gives some of the data for these conclusions as regards very common wild or garden plants, in reference to the number of stomata in a square millimetre on each side of the leaf, and the length of the stomata in each species in fractions of a millimetre. The table is made up from the measurements given by the authors mentioned.

I. Terrestrial Plants.

A. *Herbs and under-shrubs with their leaves:*

	UPPER SURFACE.	UNDER SURFACE.	LENGTH, IN FRACTIONS OF A MILLIMETRE.	
Lolium perenne, L.,	65	40	.040	to .050
Hordeum murinum, L.,	40	45	.037	.043
Polygonatum vulgare, Derf.,	0	65	.030	.033
Echium vulgare, L.,	190	190	.026	.030
Chenopodium vulvaria, L.,	65	85	.023	
Tagetes patula, L.,	43	70	.036	.050
Impatiens Balsamina,	55	95	.030	.030
Pulmonaria angustifolia, L.,	25	85	.033	.040
Euphorbia helioscopia, L.,	very rare	50	.027	.030
Mercurialis annua, L.,	0	65	.027	
Parietaria officinalis, L.,	0	100	.027	
Hypericum perforatum, L.,	0	165	.023	
Teucrium Chamædrys, L.,	0	225	.026	
———— Scorodonia, L.,	0	150	.020	.026
Fragaria virginiana, L.,	0	110	.020	.023
Calystegia sepium, R. Br.,	very rare	50	.030	.033
Helianthemum vulgare, Gœrtn.,	30-40	85-100	.026	.036

---

[1] Bulletin de l'Académie royale de Belgique, 2e sér., xvi.

[2] Op. cit., 106-109.

B. *Herbs with fleshy leaves.*

	UPPER SURFACE.	UNDER SURFACE.	LENGTH IN FRACTIONS OF A MILLIMETRE.	
Portulaca oleracea,	45	20	.046	.050
Sedum reflexum,	75 (all round)	0 (towards the summit)	.043	

C. *Shrubs and trees.*

	UPPER SURFACE.	UNDER SURFACE.	LENGTH IN FRACTIONS OF A MILLIMETRE.	
Æsculus Hippocastanum, L.,	0	175	.023	
Buxus sempervirens, L.,	0	140	.033	
Castanea,	0	175	.030	
Cerasus Mahaleb, Mill.,	0	170	.023	.040
Fraxinus excelsior, L.,	0	165	.027	
Legustrum vulgare, L.,	0	95	.030	
Lonicera pereclynium, L.,	0	65	.030	
Olea europœa, L.,	0	215	.016	.020
Quercus pedunculata, Ehrh.,	0	250	.030	
Syringa vulgaris, L.,	0	175	.027	.033
Tilia platyphyllos, Scop.,	0	150	.027	
Vitis vinifera, L.,	0	125	.030	
Protea cynaroides, L.,	25-30	25-30	.020	

D. *Resinous trees (Coniferæ).*

	UPPER SURFACE.	UNDER SURFACE.	LENGTH IN FRACTIONS OF A MILLIMETRE.	
Pinus Pinaster, Soland.,	50 (all round the leaf).			

II. Aquatic Plants.

	UPPER SURFACE.	UNDER SURFACE.	LENGTH IN FRACTIONS OF A MILLIMETRE.	
Nymphœa alba, L.,	255	0	.027	
Limnocharis Humboldtii, Rich.,	125	75	.037	
Hydrocharis Morsus-ranœ, L.,	60	rare	.040	

The *use* of the stomata was long a subject of lively controversy—Malpighi[1] regarding them as analogous to glands, and Grew[2] that they were either for the admission of air or outlets for superfluous fluid. Up to within the last thirty or forty years the glandular nature of the stomata was maintained by botanists so illustrious as Meyen and Robert Brown, neither of them believing that the stomata were furnished with a central opening. Sir Joseph Banks and Moldenhawer assisted in the discovery of their true nature; but it is to Mohl[3] that we are chiefly indebted for the complete demonstration of their function in the vegetable economy: and, wonderful to relate, all physiologists are at one on this point—viz., that their function is to give passage to air to serve the purposes of inspiration and expiration. Exhalation also takes place through them when the epidermis is too thick to prevent the escape of much moisture by direct transudation. From

---

[1] Opera omnia (1687), 142.

[2] Anatomy of Plants (1682), 153.

[3] Botanische Zeitung, 1856, 967, and trans. *loc. cit.*; and in Amer. Journal of Science, March 1857.

the section of one given in fig. 31, it will be seen that they open directly into the air-cavities,[1] which pervade the parenchyma, and thus keep up free communication with the external air and the substance of the leaf (or other organ). The cells which form the lips of the stoma are contractile, and open and close according as the leaf is subjected to wetness or dryness ; so that the evaporation of the plant is regulated according to the supply of sap it may have. It is probably owing to this fact that the stomata do not act well in direct sunshine, and that most of them are on the under side of the leaf.

Lenticels.—On young branches the surface of the epidermis is often marked by little elongated, oval or elliptical, brown, cellular rugosities, the greatest length being usually in the direction of the branch in young branches, but in old ones without any particular direction. These Guettard called "lenticular glands," and De Candolle, simply *lenticels*.[2] No traces of them are found in Monocotyledons or Acotyledons, and they are also wanting in the greater number of herbaceous Dicotyledons. They can be seen in willows, and are particularly well marked in *Euonymus verrucosus*, L. De Candolle considered that they were a sort of buds to give rise to adventitious roots ; but, thanks to the researches of Mohl[3] and Unger,[4] we know that in this idea he was mistaken.

They are formed by the development of sub-epidermal cellular tissue, which causes the epidermis to tear to give passage to them. They are situated on the periderm, and have no communication with the interior of the bark or the wood. They exist on the potato-tubercles, and are sometimes so well developed as to appear like buds scattered over the surface. Their nature is that of local developments of cork. For instance, on the birch they grow under the glands which secrete resin. In a branch of more than one year, the glands disappear, and are replaced by lenticels or tubercles of cork, which increase with the growth of the limb, and form those brown lines observed on old bark. In a word, Mohl considered that the "lenticels are analogous to cork, and are the result of a hypertrophy of the mesophlœum." Unger and St

---

[1] By funnel-shaped openings called cistomæ (κιστη, στόμα) by Gasparrini. For those remarks on the stomata see Prasitt Die Ergebnisse der neueren untersuchungen über die spaltöffnungen, "Flora," 1872, which I have only seen in abstract in the Swedish "Botaniska Notiser," 1872, s. 141-148. *Vide* also E. Pfitzer Ebenda, vii. (1870) s. 532 ; Ranter, Mitth. ber naturw. vereins of Steiermark, 1870, ii. Heft II. ; Borodin Bot. Zeitung, 1870, s. 841 ; Hildebrand Einige Beob. aus dem Gebiete der Pflanzenantomie (1861), &c.

[2] "Little lentils."

[3] Ann. des Sc. Nat., x. 33 (trans.)

[4] Ann. Sc. Nat., x. 46. He was certainly, however, in error when he considered them as in some way connected with respiration, even as obliterated respiratory organs.

Pierre[1] have arrived at very similar conclusions; but their use, if any, simple as they seem, has yet to be satisfactorily determined.

HAIRS.

(*Villi, pili.*) This name is applied to those appendages of the epidermis which resemble in external appearance, but not in structure, development, or nature, the hairs of animals. They are composed of one long cell, or of several superimposed cells. They are present in nearly all parts of the plant at one stage or another of its existence, from merely a few scattered ones to a vast number,

Fig. 37.—A unicellular stellate hair from the inferior surface of the leaf of *Alyssum saxatile*, L. — viewed from below.

Fig. 38. — Hair from the leaf of *Hippophäe rhamnoides* — seen from above.

Fig. 39.—Two branching hairs from the leaf of *Aralia papyrifera*.

---

[1] Dict. de Botanique, 830-833.

giving the plant a *villous* aspect. Sometimes the hairs are simulated by other parts of the plant, such as the pappus of the seeds of many of the Compositæ, &c.; but, as we shall see by-and-by, these hair-like organs are of an entirely different nature. They may be divided into—1. *One-celled Hairs;* 2. *Uniserial Hairs;* 3. *Pluriserial Hairs;* 4. *Glandular Hairs.*

Fig. 40.—The same seen in profile, with the cells of the epidermis on which it is carried.

1. The first, as the name implies, are formed of a single cell, simple or branched (figs. 37, 42, 44, 46).[1] 2. Uniserial Hairs are made up of several superimposed cells, arranged in a single series or line (fig. 41). After the cell of the epidermis which gives birth to this kind of hair has attained a certain stage, a transverse partition forms, and divides the cell into two equal parts. As the growth goes on, this forming of transverse partitions continues, until the hair consists of a number of cells placed end on end. Hence De Candolle called these hairs "partitioned hairs." This kind of hair can also branch, as in fig. 39 of a two-branched and stellate hair from the leaf of the Chinese rice-paper plant (*Aralia papyrifera*). Some uniserial hairs (*e. g.*, from the thistle and groundsel) have the last cell developed into a long thread-like lash.

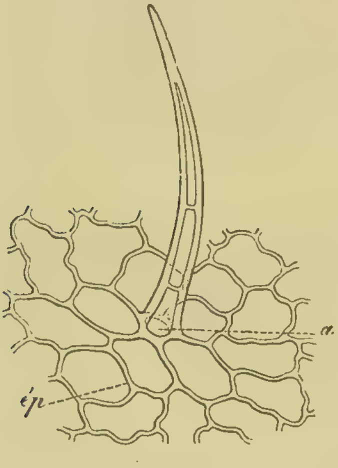


Fig. 41.—Pluricellular, uniserial hair from *Pelargonium inquinans*, Ait., with a subulate point. *a* The epidermic cell, which forms its base: *ép* The other epidermic cells in the immediate neighbourhood, with their contours feebly sinuate.

3. In Pluriserial Hairs there is a more complex structure—the cells forming several threads placed in juxtaposition and parallel (figs. 38, 40). In the figures, a front and profile view of the sea-buckthorn (*Hippophäe rhamnoides*) are given. From this it will be seen that the hair, which is in the form of a circular disc, is supported on a short column formed of cells of the epidermis. In this category of hairs, which are not only *pluricellular* but *pluriserial*, may be classed *prickles* (aculei), which are really only thickened hairs, and are distinguished from thorns by being attached, not to the wood, but simply to the epidermis—off which (as in the Rose and

---

[1] By an absurd hair-splitting refinement of nomenclature, these one-celled hairs have been classed as a particular type of cellular tissue, under the name of *Conenchyma* (κῶνος, a cone).

many other plants) they can be pulled without injuring the structure of the plant. The brown scurfy scales of the stem of ferns may also be classed as pluriserial hairs.

4. Glandular hairs are perhaps the most important of the whole four classes. This name was applied by De Candolle to all hairs possessing glands, wherever placed or of whatever nature. They appear on the surface of the epidermis in the form of cellular bodies, more or less rounded, and either resting immediately on the epidermis or raised on a very short support, as in *Robinia viscosa.* De Candolle further divides glandular hairs into—(*a*) *Glanduliferous* hairs, in which the gland is borne on the summit of the hair; and (β) *Excretory glandular* hairs, in which the gland is at the base of the hair, which in this case may be regarded as the duct by which the material secreted by the gland finds its way outwards. An excellent example of the first class is afforded by glanduliferous hair from the leaf of *Pelargonium inquinans*, Ait. (fig. 43). Again, on the chick-pea (*Cicer arietinum*, L.), there are hairs of this nature which secrete an acid liquid, considered by some chemists as oxalic, and by others—such as Vanquelin—as a mixture of malic, oxalic, and acetic acids. In the sundew (*Drosera*), the hairs secrete a sticky fluid, which stands on their tips. Hairs with glandular tips are also found on the sepals of the common flowering currant (*Ribes sanguineum*) of our shrubberies. In the tobacco-plant there are hairs with a double gland at the top, which secrete the nicotine, or active principle of the plant. In hop the bitter substance is called lupuline, and is developed by little glanduliferous bodies, called by St Pierre *Lupulins* (fig. 45). On *Geum* there is also a double gland. In the yellow snap-dragon there is a conical terminal gland with spiral markings, and in the common *verbena* the gland is rosette-shaped. In the common lavender the peculiar "bloom-like" appearance of the surface of the leaf

Fig. 42.—Stinging hair of the nettle (*Urtica urens*, L.) *b b* Is the unicellular hair itself, the base of which is swollen into an ampulla, which occupied the greater portion of the cellular support, *a b*. At the side of the figure is shown the summit of the hair more highly magnified.

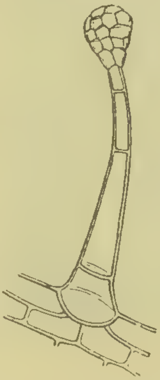


Fig. 43.—Glanduliferous hair from the leaf of *Pelargonium inquinans*, Ait., of our gardens.

is caused by much-branched hairs covering other short glanduliferous ones, which secrete and contain the perfume. In the interior of the hairs of *Drosera* (sundew) and other plants there are spiral filaments.

Fig. 44.—Hairs (*c*) and glands (*a b*) of *Rottlera tinctoria*, one of the Euphorbiaceæ. The hairs and glands cover the plant, and especially the front, with a red or reddish powdery substance, which in India and China is used as a dye and a tænifuge.

An example of the second class is afforded by the fraxinella (*Dictamnus albus*, L.), the hairs of which secrete a volatile inflammable oil. Hence, if, when the flowers are fading in the autumn, a light be applied, they are surrounded by a sort of luminous "atmosphere," caused by the ignition of this volatile oil, a fact discovered long ago by the daughter of Linnæus, but only recently confirmed and its cause discovered through the observation of Dr Hahn. Perhaps, however, the most familiar example of the excretory hair is afforded by the nettle, the type of hair to which it belongs being sometimes described as "stinging" or "urticant" hairs. It has been often described in text-books, though frequently very erroneously. Our figure (42) will explain the structure as seen in the ordinary stinging nettle (*Urtica urens*, L.) It is formed of a single cell, *b b*, which swells out inferiorly into an oval ampulla, and which, decreasing in diameter little by little, terminates in a small round knob-like point, turned slightly to one side. The base of this hair terminates in a cylindrical simple column (fig.

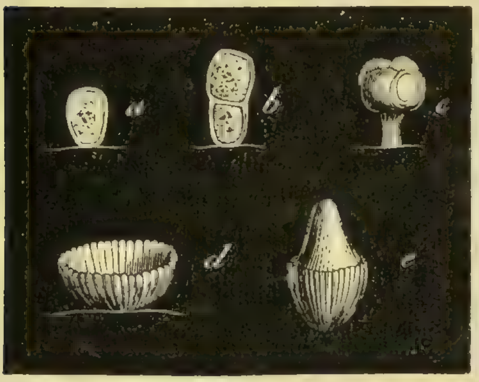


Fig. 45.—Development of the little glanduliferous organs called *Lupulins* which supply, the bitter oleo-resinous extract called *Lupuline*, characteristic of hops. *a* Lupulin commencing to form; *b* Lupulin composed of two cells; *c* Pediculated lupulin; *d* Lupulin in the form of a striated cup; *e* Lupulin completely developed.

42, *a b*), which, in order to receive the bulbous extremity of the hair (*b*), is hollowed at its superior extremity into a cuplike depression. The column, in order to form this cup, reduces its tissue from two to finally one row of cells. Meyen and most other botanists after him consider that the pedicel is the organ which secretes the stinging liquid of the hair. The hair proper is then no more than a simple reservoir for the juice secreted by the basal gland.

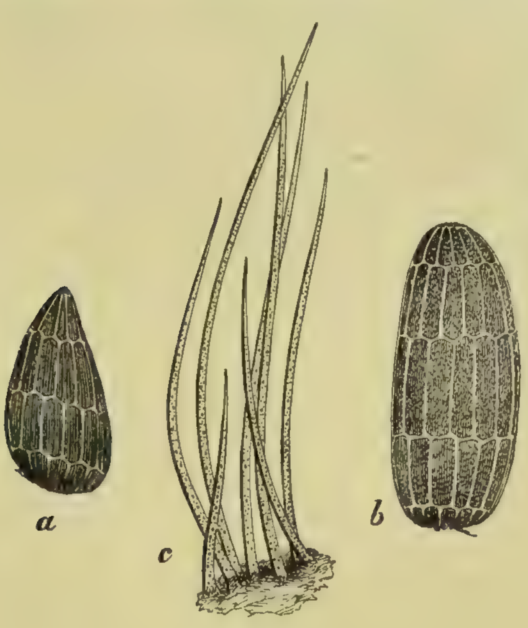


Fig. 46.—Hairs (*c*) and glands (*a b*) of another closely-allied but distinct species of *Rottlera*.

When this structure is understood, it is easy to see how the nettle stings; the very delicate transparent point of the hair is ruptured, and allows the irritating juice to escape on the part in contact with it. In *Urtica ferox*, Forst., the glandular pedicel is much longer than the hair proper. Though the acrid juice secreted by our native nettles is sufficiently disagreeable in its action, in stinging powers they are far eclipsed by some of their congeners in tropical countries. Thus *Urtica crenulata*, Roxb., stings so fiercely that it is to be avoided at all times, but especially in the autumn. Leschenault mentions that having been stung on three fingers of the hand by this species in the Calcutta Botanic Garden, the pain during two days was intense, and accompanied by tetanic symptoms; nor did he get clear of the effects until the ninth day. *Urtica ferox*, Forst., of New Zealand, will cause its stinging hairs to be held in doleful remembrance for three or four days; and Blume tells us that one species, *Urtica urentissima*, is known to the natives of Java as the *Daoun setan*, or "Devil's leaf," from the effect of its sting lasting for years, especially during moist weather. It is said to have even occasioned tetanus and death. Curious stinging hairs, often called the *Malpighian hairs*, are found in the leaves of *Malpighia*. Each is in the form of a shield, and is inserted by its middle on a mass of a glandular appearance, which secretes the stinging liquid. In some hairs (*e.g.*, from flowers of the dead nettle, lobelia, pansy, verbena, &c.) there are curious protuberances or knobs along the surface. These exist in a much exaggerated form on the hairs of the pod of the cowitch (*Macuna pruriens*), causing great irritation when the hairs come in contact with the skin.

To recapitulate in a synoptical form the chief forms of hairs, they may be classified as follows:—

I. Simple or Lymphatic.

- 1. Unicellular,
  - Simple.
  - Bi-trifurcate.
  - Branched and stellate.
- 2. Pluricellular.
  - Uniserial,
    - Simple.
    - Branched.
  - Pluriserial,
    - Cylindrical,
      - Simple and smooth.
      - Dentate or barbed.
      - Peltate or shield-shaped.
    - Flat,
      - Scurfy.

II. Glandular Hairs.

- 1. Glanduliferous, or with a terminal gland
  - Simple,
    - Capitate.
    - Cupulate.
  - Branched,
    - With many heads.
- 2. Excretory, or with a basilar gland,
  - Inoffensive.
  - Stinging,
    - Needle-shaped.
    - Peltate.[1]

The following technical terms are often met with in describing hairs. They are given without reference to the foregoing classification, simply because the same term is often used to describe the external appearance of a hair, without regard to its internal structure or functions—on which two characters the above classification is based :—

1. *Stellate*, when in a star-shaped form (Deutzia scabra). 2. *Moniliform* or beaded (Lychnis chalcedonica). 3. *Lepidote* or scaly (Elceagnus). 4. *Ramaneta* or rametaceous hairs, as in the scales on the lower part of the stem of ferns. 5. *Reticulate Hairs* or *Mattulla*, on palms. 6. Prickles or aculei. 7. *Setæ* or *Stiff Hairs*. 8. *Clavate* or club-shaped. 9. *Capitate*, with a distinct rounded head. 10. *Scabrous*, with slight projecting surface, giving a roughness on drawing the leaf or other organ over the skin. 11. *Uncinated* or hooked. 12. *Glochidiate* or barbed, with one or more points round the apex. 13. *Peltate* or shield-shaped (Malpighia, various Cruciferæ).

The descriptive names applied to organs from the presence or

---

[1] Duchartre, *op. cit.*, 101.

absence of hairs, or from their situation, are chiefly connected with the leaf, and will be given when we come to enumerate the technical terms used in describing that structure.

GLANDS.

To pass from glands to glandular hairs, or *vice versâ*, as we have for the sake of convenience done, is a natural transition. A gland, the advanced student scarcely requires to be told, is a secreting organ formed of cells, and situated in various portions of the plant, in order to perform certain functions more or less essential to the life of the plant.

The pedicellated glands, or glandular hairs, we have already described. The other and more typical ones are situated sessile on the surface of the epidermis. They generally contain oil or colourless resinous substances. These glands often appear on leaves like transparent punctations, as on the leaves of St John's wort (*Hypericum perforatum)*, rue, orange, &c. They secrete many of the distinguishing products of different plants—*e.g.*, honey, as in the " nectariferous " glands at the base of the petals of many flowers, which are, properly speaking, cavities surrounded by secreting cells; the "ice" of the ice-plant (*Mesembryanthemum crystallinum*), so called from the presence of drops of fluid on the leaves, as if they were covered with minute frozen dewdrops. In *Rochea falcata*, the surface of the ordinary cuticle is nearly covered with a layer of large prominent isolated cells, which have probably a secreting power of a similar nature to that of the plant just mentioned.

Glands are composed of a group of cells, which sometimes leaves between a space where the liquid gathers. In shape they are oval, round, flattened, &c., and are found in great numbers in plants—the same plant often containing several different forms. They have been particularly studied by Guettard,[1] Meyen,[2] and Mirbel,[3] to whose elaborate researches the student is referred for longer details. The latter botanist divides them into two classes: *vascular glands*, into the composition of which cells and vessel unite; and *cellular glands*, formed of cellular tissue alone.

In at least three species of the Ericaceous genus *Gaultheria* (*G. procumbens*, *G. Shallon*, *G. ovalifolia*), George Lawson has described[4] (and the observation has been confirmed by myself several

---

[1] Observations sur les plantes (1847); and Mém. de l'Académie des Sciences de Paris, 1847.

[2] Über die Secretions—Organe der Pflanzen, 1837.

[3] Annal. du muséum d'hist. nat., ix. 455; and Mém. de l'Instit., 1808, 344.

[4] Trans. Bot. Soc. Edin., xi. 166.

years ago) long terete brown glandular processes, each arising from a larger base on the teeth of the leaves; and in the case of *G. Shallon* and *ovalifolia* on the under surface of the leaf also, though in a less marked manner.

RECAPITULATION.

The tabular views given at the end of the various chapters of this section (I.) render any recapitulation, beyond a few words, to link the leading ideas together, unnecessary. 1. We have seen that the primary organic element of all plants is the cell—this cell being normally globular in shape, but in general more or less angular, from the pressure of the other cells. 2. Its component parts are the nucleus and nucleolus swimming in a protoplasmic fluid, and the primordial utricle lining the interior of the cell-wall. 3. In addition, the cell contains chlorophyll, starch, crystals, sugars, gums, oil—in a word, the various products for which plants are distinguished. 4. By the irregular deposition of the encrusting materials inside the cell-wall—cellulose, lignine, &c.—the cell receives various markings—dots, bars, spirals, &c.—which distinguish cells into different classes. 5. By increase and union, cellular tissue is formed. 6. The original cell is formed as follows, our knowledge on the subject of which may be summed up in Unger's words: (*a*) The young cells develop freely in the interior of the mother cell without the intervention of the cellular membrane. A solid body—the cytoblast or nucleus—appears in the protoplasmic fluid. This nucleus gathers round it, by the condensation of the exterior of its substance, the primordial utricle—which in its turn forms round it the cell-wall proper, composed of cellulose—the fluid now interposing between the nucleus and the primordial utricle, which acts as a lining to the cell-wall. (*β*) The cells are formed by the segmentation of the mother cell, which is accomplished in three distinct processes: *a*, The new membranes develop themselves from the interior of the generative membrane; *b*, The mother membrane forms folds stretching into the interior; *c*, The mother cell separates itself by constriction. 7. Lacunæ are sometimes formed in the midst of cellular tissue. 8. Communication between cell and cell is accomplished by endosmose and exosmose, or perhaps by minute openings. The thinner unthickened portions of the cell-wall also assist in this transmission of fluid. 9. When the cells elongate, get thickened with lignine, and splice over each other as in the chief mass of wood, &c., they form woody or ligneous tissue. This woody tissue is also distinguished by various markings, especially by the discs found so invariably in Coniferæ and certain other trees. They are not, however, true vessels.

10. Vessels are formed by the union of rows of cells, the partitions between which have been absorbed, so that a continuous tube remains—this tube from its origin being naturally characterised by all the markings found in the particular kind of cells out of which it has been formed. 11. Vessels also, by their union, assist in forming woody bundles. 12. The epidermis is a semi-compound organ, the simplest product of the union of cells. It covers every portion of the plant exposed to the external air (except the stigma), and even some organs not so exposed. It is composed of a structureless cuticle or pellicle, and a derma composed of one or more layers of cells lying immediately under this. 13. The appendages of the Epidermis are : (α) The stomata, opening in the surface for the admission of air and other uses, which will be particularly considered while discussing the function of the leaf; (β) Hairs of various shapes formed of one or more cells ; (γ) Glands ; and (δ) Lenticels, little cellular rugosities, the nature of which is but imperfectly known.

It thus appears that the cell is a perfect organism in itself, and that from its modification or union all the complicated organs of the plant are formed. To borrow the illustration of Schleiden, what in vegetable anatomy appears progress is in reality nothing more than development in the true sense of the word—a division, or analysis simply into a greater number of the parts composing the whole. The number 100 is a simple number ; in its development it is possible to describe it as $99 + 1$; $3 \times 33 + 1$; $3 \times (32 + 1) + 1$; $3 \times [(4 \text{ times } 8) + 1] + 1$, &c. We are able to analyse the proportions which it contains, and in place of 100 united, to establish a most complicated calculus, the final product of which will be always 100. The same is true of all nature.

SECTION II.

NUTRITION.

We now come to consider the compound organs and their functions. We have seen that a cell is a life in itself, performing every function of a perfect plant—nutrition and reproduction. We shall now see that in the highest plants these two functions require a more complicated series of organs. First, therefore, it behoves to consider the organs of Nutrition. These are the root, stem, and leaf. It will therefore be necessary to describe them before discussing the food of plants, and the method by which this food reaches the different parts of the plant and gets assimilated within its structure. Perhaps it may be more convenient to commence our description with the stem.

CHAPTER I.

THE STEM.

The Stem (caulis), *or ascending axis*, is that portion of the plant which rises above the medium from which the root—its continuation, and, in some respects, its subterranean counterpart — absorbs the nutriment; and as the rootlets spread through the soil from the main axis of the root for this purpose, according to a fixed law of arrangement, in like manner the leaves borne on the stem or its ramifications, according to a similar mathematical law, expose themselves to the influence of the air and light, to absorb and elaborate certain other nutritive materials required for the life of the plant; and finally, it bears the flowers, the perfection of which is essential to the reproduction of the plant. All these organs are more important to the life of the plant than the stem itself. The juices absorbed by the root are also conveyed through the medium of the stem to the organs named. On this view Richard has called the united stem and root the *axophyte;* and certain other botanists—Nees, for example—have styled this, while in the embryo, by the very unnecessary term of *blastema.* This "axophyte" has certain appendicular organs, leaves, &c.; but before considering them, we shall discuss the nature, structure, development, and modification of the stem.

Absence or existence.—It is not always present in plants. For instance, in some low orders of cryptogams, such as lichens, fungi, &c., it is absent; and even in mosses and some of the larger algæ, though apparently present, it does not fulfil the same physiological purposes as in the higher plants. Stemless plants (*e.g.*, dandelion) are called *acaulescent* (*α*, privative; *καυλός*, stem), in contradistinction to the *caulescent* or stemmed plants. These terms, though often loosely applied, and not perhaps strictly correct (for in descriptive botany a plant is often styled *acaulescent* which is not really so, but only with a very much shortened or indistinct stem), are sufficiently convenient to be preserved. If, as in all herbaceous plants, it is very short, and produces annually young branches, which live for a season and then perish, it is called the *crown of the root.*

Size.—The stem varies much in size, from a mere thread in some plants to from fifteen to thirty feet in diameter in the *Sequoia gigantea* of California; and from being so short that the leaves seem to spring from the head of the root, to a length of 330 feet in the gigantic tree just mentioned, and an almost equal height in some other conifers.[1] Nor does the length invariably bear any proportion to the thickness. The stem of *Calamus rudentum*, L., is often 900 feet in length, creeping along the ground, and rarely attaining a thickness of more than 1½ or 2 inches. Stems are often classed into three categories: 1. The *culm* (culmus), herbaceous or woody, generally simple, with well-marked elongated nodes; *ex.* grasses and sedges.[2] 2. The *trunk* (truncus), characteristic of most of our ordinary dicotyledonous trees, such as the oak, chestnut, elm, poplar, &c. Here the stem is usually divided after a certain distance, and ramified into smaller subdivisions called *branches*, and these again into *branchlets* and *twigs*. 3. The *stipe*[3] (stipes) or *caudex*, another kind of woody stem observed in the great division of plants called *monocotyledons*, and specially in the palms, *Yucca*, *Dracæna*, *Pandanus*, &c. The tree-ferns may also be said to have stipes. They are generally simple, cylindrical, often thicker at the summit than at the base, and in structure have the character of the monocotyledonous or *endogenous* stem, which will be presently described.

Consistence.—Taking the substance of the stem into consideration, it may be *herbaceous*, as in most plants familiarly called herbs; *ligneous*, or woody, when woody fibre forms its greatest bulk, as in trees and shrubs; a third class may be partly woody and partly herbaceous—*i.e.*, the perennial stem may be woody, but the branches which it puts out yearly, and which are only annual, are herbaceous. Such stems are called *fructicose* or *semiligneous*, and the plants themselves under-shrubs. This leads us to speak of certain terms applied to the plant in reference to its height or thickness. There are: 1. *Herbs* (sing. herba), in which the stem is completely herbaceous; 2. *Under-shrubs* (suffrutex), *ut supra;* 3. *Shrubs* (frutex), in which the stem is completely ligneous, is branched at the base, a little elongated, and less than five times the height of a man. Between shrubs and trees there are all gradations; and if the shrub approaches to the size of a tree, it is

---

[1] The writer has examined a felled tree of *Abies Douglasii* in North-West America which measured 320 feet in length.

[2] This can be well seen in the bamboo. Physicists have shown that in this hollow culm there is the greatest amount of strength combined with the smallest expenditure of material, and that the transverse diaphragms at the nodes add to the strength of this long slender stem. It is said that it was the study of this stem which suggested to Robert Stephenson the idea of tubular bridges, such as that which he afterwards threw over the Menai Strait.

[3] Also applied to the stalk of an ovary.

called *arborescent*, just as the under-shrubs are called *suffrutescent*, or *suffruticose* if less decidedly woody than ordinarily. 4. Trees (arbor), in which there is a true trunk not branched at the base, and which attains at least five times the height of a man. 5. *Bushes* may be defined as low, much-branched shrubs. Numerous other terms are used to express the form, composition, and direction of the stem.

Division of stems according to structure.—There are three great classes of stems corresponding to those three great classes into which plants have been divided.

The first is the *Dicotyledonous* (δὶς, twice; and κοτυληδὼν, a seed-lobe) or exogenous stem, which shows on a transverse section concentric layers of wood surrounding a pith, and the wood again surrounded by a detachable outside bark. The plants of which this stem is characteristic have also two lobes to the seed, which seed, on first sprouting, sends up two seed-leaves or cotyledons above ground—hence the name of the class—and have, in nearly every case, their leaves reticulated or netted-veined. From increasing in thickness by additions of layers of wood—one being yearly superimposed above that of the previous year—they are called *Exogenous* or outside growers (ἔξω, without; and γίνομαι, to grow). All our British and temperate forest-trees have stems of this type.

2. The second class is the *Monocotyledonous* (μόνος, one; and κοτυληδὼν) or endogenous stem, in which there are no concentric layers of wood, no pith, and no detachable bark, and in which the embryo has only one seed-lobe, and the leaves are parallel-veined. This stem increases in thickness by deposition of wood-bundles from within outwards, and hence has been called *Endogenous* (ἔνδον, within; and γίνομαι). The palm-tree stem is a typical example of this description of stem.

3. The remaining division of stems is the *Acotyledonous* (α, privative; and κοτυληδὼν) or *Acrogenous* (ἄκρος, summit; and γίνομαι) stem, in which the young plant springs from a spore, and has no true seed-leaves, in which the stem or stipe increases in thickness by the union of the bases of the leaves or fronds, and in which the venation is forked. The tree-ferns have stems of this kind. This classification is not an artificial one, but is founded on nature—each stem, as we have seen, finding corresponding differences in other portions of the structure, and in the development of the three great classes of plants to which it belongs. To recapitulate in tabular form, the three kinds of stems are as follows:—

1. **Dicotyledonous** or EXOGENOUS = two cotyledons,—netted-veined leaves = increase from without inwards.

2. **Monocotyledonous** or ENDOGENOUS = one cotyledon,—parallel-veined leaves = increase from within outwards.

3. **Acotyledonous** or ACROGENOUS = no cotyledons, — forked-veined leaves = increase at the summit by the remains of bases of the leaves.

STEM OF DICOTYLEDONS.

In the embryo (or plant as it exists in the seed) the future stem is represented by the part between the attachment of the two cotyledons superiorly, and the radicle inferiorly—the first of these two points being known as a *node*, the next as the *collum*, and the interspace between them the *internode*.[1] These parts are more marked in the developed plant, and go under the same names, the nodes giving attachment to the leaves, and the stem increasing by the development of these internodes, each internode representing a year's growth.

Buds.—The *Gemmule* (plumule, Link[2]), or young bud (*gemma*), which terminates the young stem, is therefore the growing or vegetative point.[3] This vegetative point develops successively a series of internodes, each terminated by one or more leaves. In the terminal buds at the end of the stem—often the whole element of next year's growth—leaves and nodes can be seen, only requiring the elongation of the internodes to fully expand, as is shown in figs. 47, 48, 49, 50. A bud is therefore, in the language of Gray, "nothing more than the first stage in the development of a stem, with the axis still so short that the rudimentary leaves within successively cover each other, while the whole is covered and protected by the scales without. As the bud is well supplied with nourishment in spring by the stem on which it rests, its axis elongates rapidly; and although the growth commences with the lowest internode, yet the second, third, and fourth internodes, &c., have all begun to lengthen long before the first has attained its full growth. The stem, thus continued from a *terminal* bud, is, if it survive, again terminated with a similar bud at the close of the season, which in its development repeats the same process." The rings (fig. 47, *a*) mark the limits of each year's growth, and are the scars left by the fall of the bud-scales. In trees with strong buds, like the horse-chestnut, they may be traced back for a number of years, until the distention of the stem and the weather have obliterated them. On the horse-chestnut, &c., can also be

---

[1] Dupetit, Thomas, and others, have called this the *merithallium* (μερὶς or μέρος, part; and θαλλὸς, stem). Irmisch has also called the first internode, which terminates at the attachment of the cotyledons, the *hypocotylonaxis*.

[2] Link has also given the term *gemmula* to a form of leaf-bud; and in addition, Schleiden and Endlicher are almost alone in applying it to what is termed by nearly all botanists the *ovule*. Linnæus gave all buds the name of *hybernacula*, from their use in continuing the plant life through the winter. He divided them into—1. Buds proper, 2. Bulbs.

[3] The *punctum vegetationis* of G. Fr. Wolff.

seen, after a long time, the scars left by the fall of the leaf, the "dots" marking the place where the woody bundles composing the petiole separated (figs. 47, 50). Buds vary considerably in their nature and size. In some plants they are covered by the bark until spring. In these cases the elements composing them are in their dormant condition, not very distinct. In many plants, as in herbs and very many tropical trees, and in some shrubs of temperate latitudes (*Rhamnus frangula, Viburnum lantana*), they are

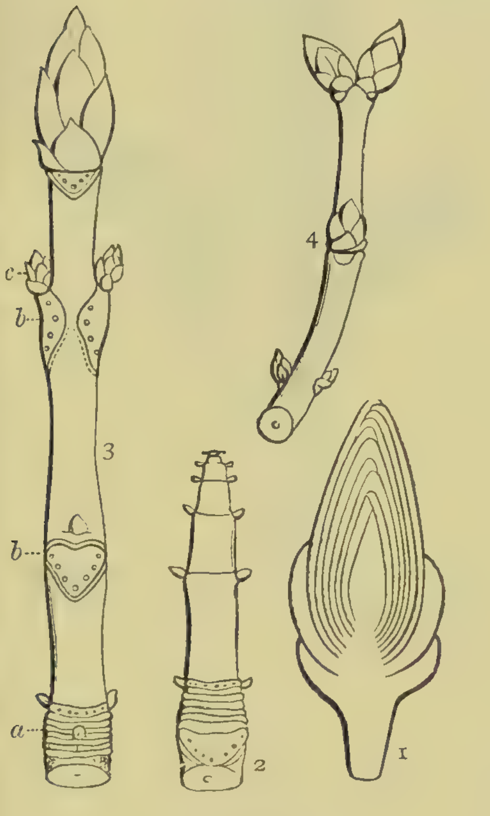


Fig. 47.

1. Diagram of the vertical section of a spring bud, such as that of the horse-chestnut.
2. The axis of the same developing, the elongation beginning with the lowest internode, soon followed by others in succession.
3. A year's growth of the horse-chestnut, crowned with a terminal bud. *a* Scars left by the bud-scales of the previous year; *b b* Scars left by the fallen petioles or leaf-stalk; *c* Axillary buds.
4. Branch and buds (all axillary) of the lilac (after Gray).

Fig. 48.—Branch of cherry carrying intermingled a number of buds, some for the flowers, *b b b*; the others for the wood, *b' b' b'*.

naked, while in others they are covered with scales which envelop and protect the delicate structure from rain and sudden changes of temperature at a season when it can ill withstand such. In some the bud is covered with a gummy, waxy, or resinous exudation, which wards off rain; while in a fourth kind of bud the interior is lined with a non-conducting kind of down or wool, which serves the purpose of protecting the young leaves and other structures from cold during the winter season.

Fig. 49.—Extremity of a branch of the lilac (*Syringa vulgaris*) with two opposite terminal buds, and almost at the summit of which are found two lateral buds. This branch, then, cannot be prolonged in a direct course.

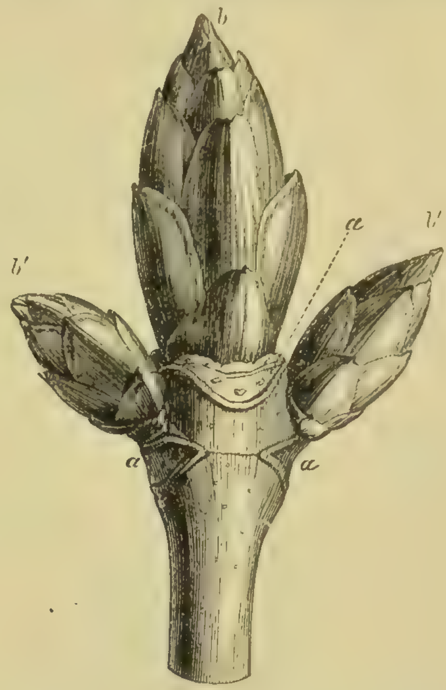


Fig. 50.—Extremity of a branch of the horse-chestnut (*Æsculus Hippocastanum*, L.) bearing a large terminal bud, *b*, and two rather smaller lateral buds, *b′ b′*; *a a a* Cicatrices left by the fallen leaves.

The *terminal* bud (fig. 50), which many trees and shrubs habitually produce, is thus a direct continuation of the stem or branch; but there are also *lateral* buds produced in the axils of leaves, (figs. 47, 49, 50). Some trees and shrubs do not produce the terminal bud, and in this case their place is taken by lateral ones, unless as, for example, in the lilac (fig. 49), the axis is terminated by two opposite buds produced at its truncated extremity. On the other hand, palms and most monocotyledons produce no lateral buds, and the stem must be therefore continued upwards by the terminal bud. In general, each leaf of those shrubs and trees which produces axillary buds, produces but one in its axil; and accordingly, the arrangement of the branches on the trunk and the twigs on the branches must be the same as the arrangement of the leaves—that is to say, the branches are opposite on plants with opposite leaves, alternate on plants with alternate leaves, and so on. There are a few exceptions (as in certain species of *Cuphea*, in which the leaves are opposite or verticillate, but the ramifications alternate), but the main principle enunciated holds true in the great majority of plants. There are, however, certain natural orders (Scrophulariaceæ, Acanthaceæ, Solanaceæ, Rubiaceæ, &c.) which have habitually several buds in the axil of each leaf, all ranged longitudinally along the axis, the upper ones more advanced than the lower ones.[1] In addition to the *regular* terminal and axillary buds, there occasionally appear *adventitious* ones on indeterminate parts of the stem, and even on leaves.

These *bud-scales* (which Mirbel called as a whole *perula*) are again only modified leaves; they have the same structure and arrangement as the leaves proper of the plant, and graduate by insensible transitions to these in many plants. The *turions* or subterranean budding-shoots of many perennial herbs, and the unfolding buds of the lilac myrtle (*Vaccinium myrtillus*), show every gradation between the bud-scales and the foliage—proving that there is no absolute line of demarcation between them, but that they are only modifications of the same organ to subserve different purposes. Such buds, only covered with the ordinary leaves remaining in an imperfectly-developed state, are termed *foliaceous* buds. Again, the base of the petiole may be modified so as to serve the part of scales (*petiolar* buds), while the name of *stipular* buds is applied to those in which the stipules play that part (*e.g.*, in various fruit-trees, beech, &c.) Lastly, in the roses, where the stipules are united to the sides of the petiole, both the petiole and stipules are thus conjoined in the office of protecting the young bud; in these plants the scales may be distinguished as *fulcrar*[2] (Duchartre). Most frequently the terminal bud, which opens in spring, develops into a shoot bearing leaves alone, but in other cases it may bear flowers, while in a third case some plants are provided with buds which produce both flowers and leaves (the vine, for example). The first are accordingly called *leafing or wood buds;* the second, *flower or fruit buds;* while the name of *mixed buds* is applied to the last (fig. 48). It is not difficult to distinguish the flower and leaf buds. The first are large, swollen, ovoid, and more or less obtuse; while the second are straight and pointed, as shown in the apple, pear, or cherry (fig. 48). Though in their earliest stage they do not materially differ either internally or

---

[1] Guillard, Bourgeois, and Damaskinos: Bull. Soc. bot. de Fr., iv. (1857) 957 *et seq.*, and v. (1858) 598-610.

[2] Under the name of *fulcra*, Linnæus included stipules, bracts, spines, tendrils, and even hairs and glands.

externally, as a rule there is a determinate number of scales for the buds of each species of plant, and also an equal determinate number of leaves developed by the shoot.[1] Lastly, it may be mentioned that though the buds of woody plants present the utmost variety, both in position and form, yet it is possible, even in the depth of winter, to recognise each species by its buds alone. This has actually been done.[2]

Ramification or Branching of Stems. — If the stem grows without branching, simply through one terminal bud, it is a *simple* stem. Short dicotyledonous stems, however, ramify into numerous subdivisions in the following manner: Each leaf, when it joins the stem, forms with the stem an angle more or less acute, which is the *axil*, just as the arm-pit is the axil at the union of the trunk and the arm. This axil has the power of forming *axillary buds*, which buds have all the characters of the terminal bud, and can continue the axis in the form of branches, just as the terminal bud can the main axis. This bud accordingly forms nodes and internodes in the manner already described, and it again is subdivided in the same way, until the branched character so familiar to us in ordinary trees like the oak or elm is given. The stem from which the first branches spring is, accordingly, the *primary axis*, and the branches springing directly from it the *secondary axis*, or the axis of the second degree; and those from it again the *tertiary* axis, and so on; or, in familiar language, the tree has a branched trunk, with branches, branchlets, and twigs. The extent and mode of ramification differs in different species of trees and other plants, giving to them their various habits and physiognomies.[3]

Twining Stems.—Many plants, particularly of herbaceous species, have stems which support the plant in an erect position by twisting themselves around the stem of some stouter plant in its neighbourhood; and it is a most curious fact, which will be further touched on (Section IV.), that the direction in which they twine is always the same in each species, no matter under what conditions the species may be placed. For instance, the hop (*Humulus lupulus*, L.) and honeysuckle (*Lonicera*) twist towards the left hand (standing in front of the plant), a direction expressed in systematic works by

---

[1] Ohlert, Linnæa, 1837, 632-640.

[2] Moritz Wilkomm, Deutschlands Laubhoelzer im Winter, 1859.

[3] Humboldt on the physiognomy of plants in "Views of Nature" (Bohn's Trans.) p. 210. A most exhaustive treatise on the ramification of flowering, principally in relation to the division of the vegetative point, has been published by Dr Eugene Warming of Copenhagen, in the Transactions of the Danish Academy of Sciences (1872), entitled "Forgreningsforhold hos Fanerogamerne betragtede med særligt Hensyn til klövning af Vækstpunktet" (pp. 164, with *résumé* in French, 11 plates and 15 woodcuts), to which I can only refer the student.

the sign ☾ (*sinistrorsum volubilis*). On the contrary, in the Chinese yam (*Dioscorea Batatas*, Dcne.), the haricot (*Phaseolus vulgaris*), *Dolichos*, the great hedge bearbind (*Calystegia sepium*, R. Br.), &c., the twisting is towards the right, and is expressed by the sign ☽ (*dextrorsum volubilis*).

Fleshy Stems.—The stems of some plants, particularly of the order *Cactaceæ*, are large and fleshy, taking the most *bizarre* forms, and differing entirely in appearance from what is ordinarily understood as such in other dicotyledonous plants. For instance, in *Echinocactus ottonis*, Lehm. (fig. 51), the flower is absolutely longer than the stem is high. In *Opuntia Dillenii*, Haw. (fig. 52), the stem, which at first is almost cylindrical at the base, swells out into oval-flattened expansions, which look as if they were articulated one above another.

Fig. 51.—*Echinocactus ottonis*, Lehm., entire plant.

Cladodia.—In the last-named species of cactus, the peculiar form of the stem approximates it to what Martius called a *cladodium*[1]—a form of branch which simulates a leaf by reason of its abnormal form and green colour. The cladodium presents a certain analogy with the teratological phenomenon called "fasciation," with this difference, however, that the cladodium is normal, with rounded or even angular extremities, and that the form is regular and constant in the same species. A good

---

[1] Κλάδος, branch.

example of this form of branch is afforded by the common butcher's-broom (*Ruscus aculeatus*) fig. 53, and in the genera *Phillanthus* or *Xyllophylla* belonging to the order Euphorbiaceæ. The thread-like branches of the common Asparagus (*Asparagus officinalis*) are also examples of cladodia. Vulgarly, these cladodia are looked upon as leaves, but in asparagus, as in butcher's-broom, the true leaves are in the form of minute scales; and if we consider, as St Pierre does, the joint and stem of *Opuntia Dillenii* (fig. 52) as also belonging to this type, we must look for the leaves in the spines on the cladodia.

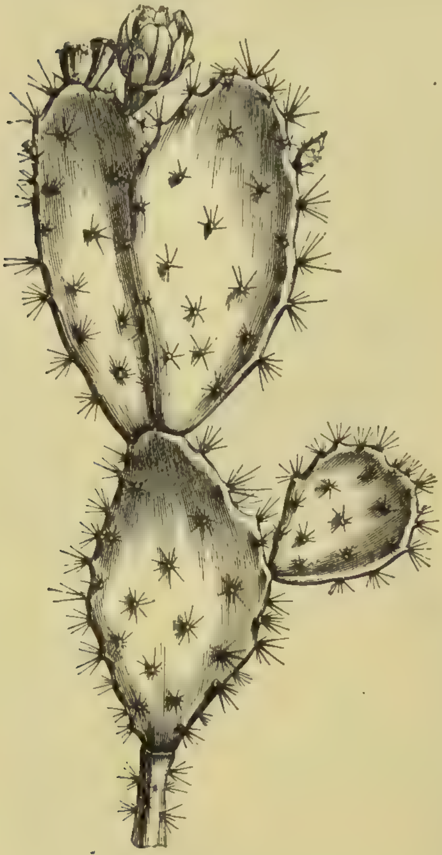


Fig. 52.—Flowering branch of *Opuntia Dillenii*, Haw.

Fig. 53.—Flowering branch of the butcher's-broom (*Ruscus aculeatus*, L.) *cld cld* Cladodia twisted on their bases (*a*) in such a manner as to have their planes almost vertical; *fl fl* Flower borne on the median line, and on the upper aspect of the cladodium.

Structure of the Stem: Development.—In the earliest state of the stem, its structure is extremely simple, being merely a mass of parenchyma, surrounded by a delicate epidermis—this parenchyma being divided into a central mass and a peripheral layer by the interposition of a layer of very minute cells. This central cellular mass, which is out of proportion to the diameter of the stem in its size, is the first trace of the pith. The peripheral layer is the first stage of the bark, while the intermediate layer of delicate cellular tissue is the layer on which the future growth and increase of the woody zones and bark depend — in a word, that which goes under various names,[1] but is most commonly known as the *cambium* layer of the stem.

Very soon after the stem has passed out of the embryo state, some of the cells begin to lengthen into tubes, and to become marked with transverse bars or spiral lines, and thus give rise to ducts or vessels; these form a small and definite number of bundles or threads, say four equidistant ones at first: surrounding these, other slender cells of small calibre, and destitute of markings, soon appear, and form the earliest woody tissue. As the rudiments of the next internode and its leaves develop, two or more additional threads of vascular tissue appear in the stem below in the parenchyma, between the earliest-formed ones, and are equally surrounded with woody tissue. Thus, at an early stage, these bundles of woody tissue thus formed increase and enlarge, and run together to make up a woody zone, which looks, on a transverse section, like a ring enclosing the central part of the parenchyma, and itself enclosed by the external parenchyma, and so situated in the original homogeneous cellular system as to divide it into two parts — namely, a central portion, which forms the pith, and an exterior portion, which belongs to the bark. The whole is invested by the epidermis or skin, which covers the entire outer surface of the bark. The woody masses or wedges are separated from each other either by lines or bands of the original cellular tissue, which pass from the pith to the bark, and which necessarily become narrower and more numerous as the woody bundles or wedges increase in size or number. These are the *medullary rays*[2] (fig. 55).

Fig. 54.—Cladodium of *Phyllanthus* (Xylophylla) *montana*, Sw., the edges of which are marked with patent teeth, carrying little scales (semi - abortive leaves) and a flower in all the teeth.

---

[1] It is the *Zone génératrice* of Mirbel, the *Bildungsschicht* of Meyen, &c., *couche sous-liberiénne* or *Endoderm* of Richards, and *Verdickungsring* of Schacht. Duhamel, to whom we are indebted for the term *cambium*, did not employ it in exactly the same signification as modern botanists; but this is of no consequence.

[2] Gray, Structural and Syst. Bot., 117.

The first year's growth of the stem of a dicotyledonous plant consists accordingly of three principal parts: first, an interior cellular portion or *pith;* second, one zone of *wood;* third, an exterior cellular portion or *bark* (fig. 57). The mode of growth of these we have already explained.

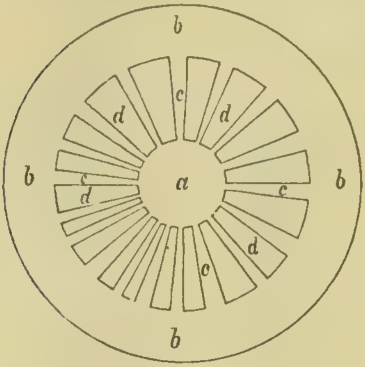


Fig. 55.—Diagram of the first formation of an exogenous stem. *a* Pith; *b b b b* Bark; *c c c c* Plates of cellular tissue (medullary rays) left between the woody bundles *d d d d* (after Carpenter).

Making now a transverse section of a dicotyledonous plant, say at the age of four years, we would see the following structure from within outward:—

1. Pith or Medulla.
2. Medullary rays—radiating lines coming from the pith out to the bark.
3. Medullary sheath surrounding the pith.
4. Layers of woody substance in concentric arrangement.
5. Cambium layer, or Endophlœum.
6. Bark composed of the following layers:—
    - α Liber or bast layer, with laticiferous tubes, &c.
    - β Mesophlœum or green layer.
    - γ Epiphlœum, suberous, or corky layer.
    - δ Epidermis.

Let us consider each of these separately.

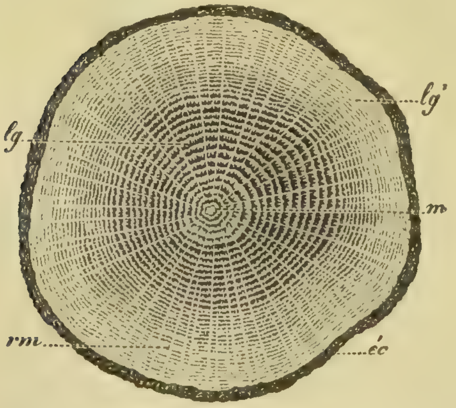


Fig. 56.—Transverse section of the trunk of an oak (*Quercus Robur*, L.), aged 37 years. *m* Pith, with a pentagonal contour; *lg lg'* Mass of wood formed by 37 annual zones; through it traverse the medullary rays, distinguished by the light lines *rm*; *éc* Entire bark.

(1.) *Pith.*—The pith occupies the medullary canal in the centre of the plant, and in the young plant is a continuous mass of cellular tissue, the cells of which are filled with sap, and of a more or less intense green colour. When the plant gets older, the juices get absorbed by the plant, and the pith becomes dry and white, tearing with the utmost facility. In some plants, such as the Walnut and Jasmine (*Jasminium officinale*), the stem increases in its young state rapidly, so that the pith gets broken, and remains in the form of fragments, forming transverse partitions in the now hollow stem.[1] In some

---

[1] Hence, in this state, sometimes called *disciform* (δισκος, a disc).

cases (*e. g.*, most Umbelliferæ) the pith is hollow or *fistulose*, and is interrupted at the nodes alone by transverse partitions. The rupture of the pith can also be seen in the clover-stalk, the rank pea-vine, and in a hollow potato-tuber. The cells of the pith are often of a perfectly regular hexagonal form. It is not uncommon, however, to find the pith pierced longitudinally by latiferous bundles (p. 42), which have been called "Medullary vessels or fibres." These can be well seen in the *Ferulas* (fennels), *Nyctora*, *Euphorbias*, &c. These vascular bundles sometimes contain a few spiral vessels, which seem to have been detached from the medullary sheath. The cells on the periphery of the pith preserve their vitality longer than those in the centre. Hence, at the end of the second year of the life of the plant, Guillard distinguished the *annular* and the *central* pith, and considered that in the former essentially vitality resided, the latter at that period being already dead. In the early state of the pith, especially when full of starch, it may perhaps assist in the nutrition of the young plant,[1] but in the dry or disrupted state it can be of no use whatever. Slices of the pith of *Aralia papyrifera*, Hook., form the rice-paper of the Chinese, just as the Papyrus of the Nile was employed for a similar purpose by the ancient Egyptians. In size and shape the medullary canal varies. It also decreases in diameter with the progress of vegetation. Though in general circular, it is sometimes elliptical, triangular, &c. Palissot de Beauvois[2] thought that he had detected a connection between the shape of this canal and the position of the leaves. For example, it is elliptical when the leaves are opposite, as in the ash; triangular when they are in verticils of three (*Nerium Oleander*), &c.: but this law presents too many exceptions to be received as established. The pith can even be extracted without the plant suffering much, if any, injury.

(2.) *Medullary Rays* (fig. 56, *rm*) are composed of muriform cellular tissue, elongated transversely (or in a direction opposite to that of the cellular tissue of the rest of the stem), rarely pointed at either extremity (fig. 4); they keep up the connection between the pith and the bark, as well as the rest of the stem, through which they probably distribute the sap. They penetrate in a stellate manner through the wood and cambium from the pith to the bark, and form the "silver grain" of the carpenter, which gives the glimmering lustre to many kinds of wood, such as maple, oak,

---

[1] The chief part of the feculent substance of the tuber of the potato and sweet potato, and of many underground stems, is pith. The starch of the yams, manioc (*Jatropha Manihot*), and "arrowroot" (various species of *Dioscorea*, *Marantaceæ*, but particularly *Maranta Indica*), is also derived from the pith (p. 26).

[2] Mém. de l'Instit., 1811.

&c., when cut so as to expose them. The medullary rays are wanting in some dicotyledons, such as the Crassulaceæ, *Pisonia*, *Lathræa Clandestina*, *Melampyrum*, &c., and are very indistinct in others (Coniferæ, &c.)

(3.) *Medullary Sheath* (fig. 60, *ms*).—This layer scarcely deserves a separate name, as it is simply the first-formed layer of woody matter containing a number of spiral ducts—the only ones found in the wood—and surrounds the pith : hence the term applied to it.

Fig. 57.

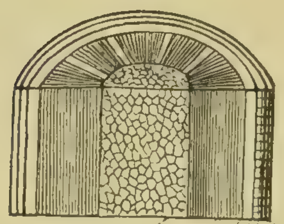


Fig. 58.

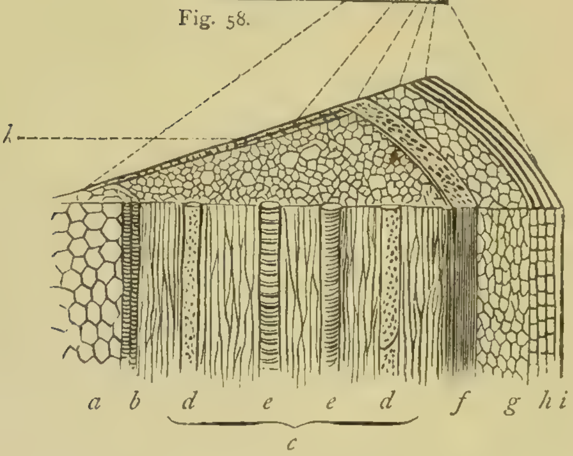


Fig. 59.

Fig. 57.—Longitudinal and transverse section of a stem of the soft maple (*Acer dasycarpum*) at the close of the first year's growth (nat. size).

Fig. 58.—Portion of the same magnified, showing the cellular pith surrounded by the wood, and that enclosed by the bark.

Fig. 59.—More magnified slice of the same, reaching from the bark to the pith. *a* Part of the pith ; *b* Vessels of the medullary sheath ; *c* The wood ; *d d* Dotted ducts in the wood ; *e e* Annular ducts ; *f* The liber, or inner fibrous bark ; *g* The cellular envelope, green bark, or mesophlœum ; *h* The corky envelope, or epiphlœum ; *i* The epidermis, or skin ; *k* One of the medullary rays, seen on the transverse section (after Gray)

If a young twig is broken through, after dividing the bark and most of the wood, the fibre coiled in the spiral ducts can be seen unrolled in the form of delicate gossamer threads. This medullary sheath is formed in the first year's growth, and is not repeated.

(4.) *Wood* (figs. 56, 57, 58, 59, 60, 61).—The wood which forms the body of the stem is composed of woody tissue, with vascular intermingled, chiefly in the form of dotted ducts, or occasionally some annular ones. It is composed of circular layers, made up of these materials superimposed one above the other to an extent practically indefinite. It will thus readily be seen that the outside layers are the youngest and the inside the oldest. Accordingly, if we examine the stem, say of an oak or walnut, we will find the wood in the interior of the stem denser and of a darker tint than the

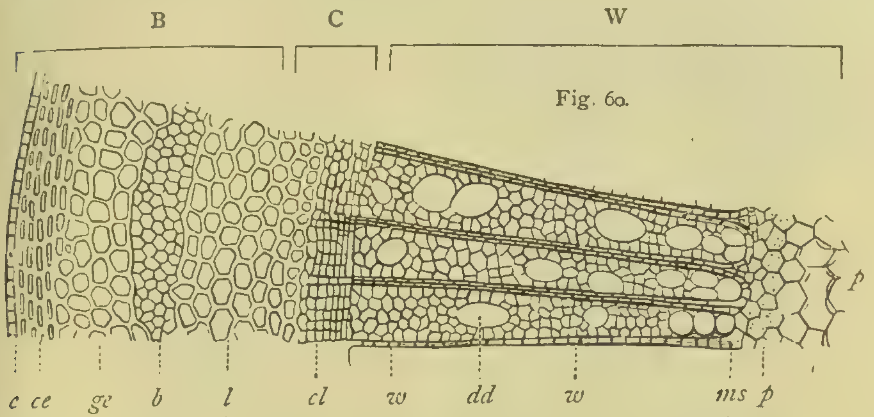


Fig. 60.

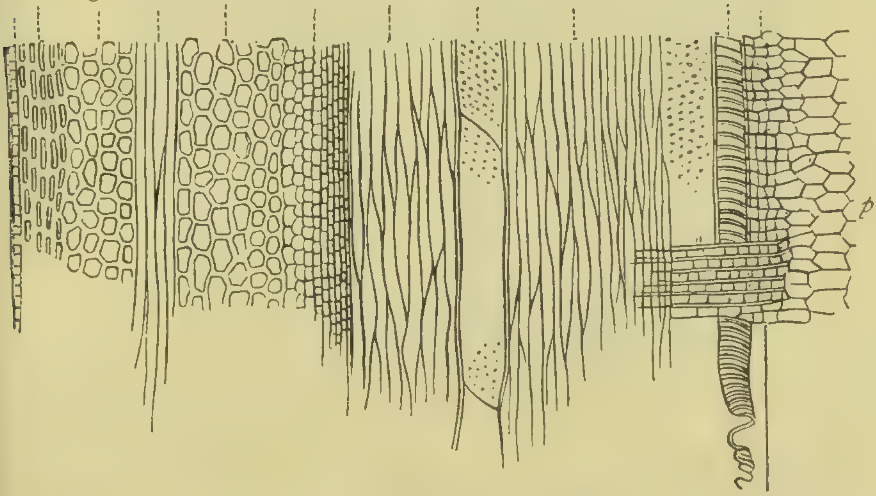


Fig. 61.

Fig. 60, portion of a transverse section, and fig. 61, a corresponding vertical section, magnified, reaching from the pith, *p*, to the epidermis, *e*, of *Negundo aceroides*, Mœnch. (the American box-elder), a year old. B The bark; W The wood; and C The cambium layer, as found in February. *ms* Medullary sheath; *w w* Wood; *d d* Dotted ducts; *cl* Inner part of the cambium layer, which begins the new layer of wood; *l* Liber—its bast-tissue, *b*, belongs to the woody system; *ge* Green envelope, or mesophlœum; *ce* Corky envelope, or epiphlœum; *mr* Medullary ray, seen on the vertical section, where it runs into the pith. In this tree we find a thick layer of parenchyma (*l*) inside of the bast-tissue, and therefore belonging to the liber. No bast-tissue is formed in it the second year. (After Gray.)

outside layers. To the first has been given the name of *Duramen* or heartwood, and to the latter *Alburnum* or sapwood. Sometimes the difference between the colour is very marked, and the change from the one to the other is made sharply, without any intermediate shades, as in the ebony or in the Campeachy wood, in which the duramen is black or dark brown, while the alburnum is almost white. In most cases the duramen becomes brown. However, in the barberry it is yellow, in the red-cedar (*Juniperus Virginiana*) red, in the Judas-tree (*Cercis*) yellow, and in the *Guaiacum* greenish. Frequently, however, especially in white-wooded trees, there is no sensible difference in colour between the two kinds of wood, as in poplars, willows, &c. These colours appear in some cases to be due to special vegetable substances mingling with the incrusting lignine, and in other instances are owing to some peculiar effect of age on the lignine. The colour will be produced often rapidly, and bears no relation to the annual increase. Occasionally it will happen that one or more of the woody rings on one side of the stem will be coloured, while the remaining half of the same rings on the other side will have the hue of the alburnum. The duramen is always of more economic value than the alburnum. Physiologically, the effect of this hardening of the duramen is to

Fig. 62.—Transverse section (much magnified) of a very small portion of the liber of *Cinchona Calisaya*. *rm' rm'* Medullary rays entering the bark ; *fl' fl'* Cortical fibres ; *cc cc* Cellular tissue (Weddell, *Quinquinas*, Pl. II. fig. 33).

render it impervious to sap, so that the heart of the tree may be removed or injured by decay without its vigour being at all disturbed.

Chemical Composition of Wood.—Payen has shown that the base is *cellulose*, which is identical in composition with that which forms the other elementary tissues of plants, but that this is changed in the course of growth by the deposition of four other substances having different properties, and capable of being isolated one from the other by different chemical reagents. These substances are: (1.) *lignose*, insoluble in water, alcohol, ether, or ammonia; soluble in potash and soda: (2.) *lignone*, insoluble in water, alcohol, and ether; soluble in ammonia, potash, and soda: (3.) *lignine*, insoluble in water and in ether; soluble in alcohol, ammonia, potash, and soda: and (4.) *ligniréose*, soluble in alcohol, ether, ammonia, soda, and potash, and also to a slight degree in water.

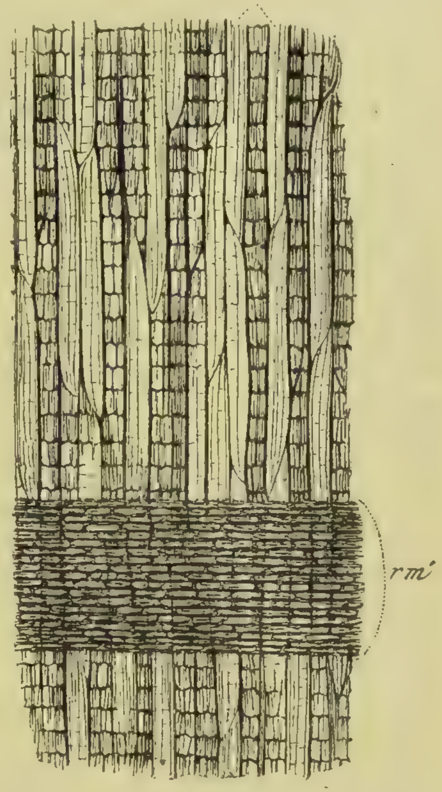


Fig. 63.—Longitudinal section of the liber of *Cinchona Calisaya*, parallel to the direction of the medullary rays *rm′*.

Formation of the Annual Zones of Wood.—As the cells of the cambium multiply, some lengthen vertically into woody tissue or prosenchyma; some are transformed into ducts; while others, remaining as parenchyma, continue the medullary rings, or commence new ones. In this way a new layer of wood is formed above that of the former year.[1] Next year the same process goes on, so that it will follow that the "rings" or concentric layers of wood displayed on making a transverse section of the stem will give the age of the tree, each layer representing one year of growth, coincident with the growth in length by the development of the body, and "continuous with the woody layer of the new roots below, and of the leafy shoots of the season above."[2] This is not, however, exactly true; because, under certain exceptional circumstances, a second layer of wood

---

[1] Hence Exogenous plants are sometimes called *Cyclogens* (κύκλος, a circle; and γίνομαι).

[2] Gray, *lib. cit.*, p. 123.

may be formed the same year by the ascent of the sap during the autumn. In a chenopodiaceous plant—*Phytolacca dioica*—Martins counted seven layers formed in one year, probably by alternate stretches of cold or warm weather. In numerous instances, as in the arborescent species of cactus, *Araucaria Brasiliensis*, *Cinchona succirubra*, *Coffea Arabica* (coffee), *Ardisia excelsa*, *Erica arborea*, &c., the wood, owing to its growth going on all the year round, forms a uniform stratum, whatever be the age of the trunk; or, as we shall see in *Cycas*, where the layers are few, and do not correspond with the age of the trunk, other exceptional forms will be presently noticed. The annual layers are most distinct in trees of temperate climates, where there is a prolonged period of repose during the cold of winter. In tropical trees the layers of wood are rarely so well marked, though in these countries there is, during the dry and hot season, a marked annual suspension of vegetable life. In temperate countries, also, a cold or wet and warm season leaves its record in a narrower or broader ring of wood in the tree. Soft-wooded trees grow most rapidly; and there is said to be a time in the life of trees when they grow more rapidly than at other times. For example, in the oak the period is between the twentieth and thirtieth year of its age.

The thickness of the woody layers also depends a good deal on climate. Bravais and Martins[1] found in a Scotch fir, aged 150 years, in lat. 48° N. lat., the average thickness of the layers was 3 millimetres 42; in lat. 60° 40′, the mean for a fir of the same age was $1^{\text{mm.}}$ 51; and that in 70° the thickness had decreased to $0^{\text{mm.}}$ 84. They found also that the compactness of the wood increased in an exact ratio to the distance north.

Causes of the different qualities of Wood.—To sum up the causes of the differences of wood, Schacht shows that these differences must be referred to: (1.) The existence of vessels which are wanting in all true coniferæ, but exist in "joint firs" (*Ephedra*, *Gnetum*, &c.), and in all foliaceous trees. (2.) The disposition, length, and size of the medullary rays, which are scarcely visible in coniferæ, being formed of only one row of cells, an arrangement also found in willows, poplars, elders, birches, hazels, horse-chestnuts, &c., while in others they are formed of several rows. Again, in most trees the rays are hardened, but in the trunks of various Cactaceæ—*Mamillaria*, *Opuntia*, and *Encephalartos*—this is not so. (3.) The presence or absence of cells or lacunæ containing resin, found so abundantly in most coniferæ—lacunæ being chiefly found in the firs, while cells containing this substance are more characteristic of the cypresses and yews, neither the one nor the other being found in *Abies pectinata* or in *Araucaria*. And (4.) the presence of a woody parenchyma, containing

---

[1] Ann. des Sc. Nat., xix. 129 (1848).

starch or other analogous products. The hardness or the weight of wood depends on the structure and development of its tissues. The induration of the cells, the number of vessels, and the presence of woody parenchyma, also considerably assist in this. Some woods, such as *Anona* (custard-apple), *Erythrina* (coral-tree), *Æschynomene paludosa*, *Carica papaya* (papaw-tree), poplars and willows, *Thuja*, &c., are very light; others are so heavy as to sink in water—*e.g.*, *Brosimum Guyanense* even when dried; while *Pinus ponderosa* when full of sap will sometimes have a specific gravity greater than that of water.

Limitation of the Annual Layers.—In oak, chestnut, &c., the outer limit of each year's growth is sharply defined by the layers of large dotted ducts, the open mouths of which can be seen so easily on a transverse section. In other trees, such as maple, where they are not so large and are scattered, and in firs, &c., where there are no ducts at all, but only punctated tissue (p. 39) throughout, the limit of each year's growth is defined by the layers of more minute and laterally flattened wood-cells, which form as the vital efforts get feeble towards the end of the growing season, and the larger cells, which commence next year's layer when vital energy is active—the two thus forming a well-marked boundary.

(5.) *Cambium Layer.*[1]—If the bark is stripped off a tree in spring a slimy slippery substance is seen and felt. This is the Cambium layer—a delicate mucilaginous tissue, full of dextrine, protoplasm, and other organisable matters, and is particularly abundant in spring when growth commences. At that season it is charged with mucilaginous sap, and accordingly the bark is then more easily separated from the wood. In autumn the cells become indurated—in fact, liber and wood cells—so that to strip off the bark smoothly is a less easy task than in the spring. But still the tissue is organically connected with both. The inner portion of the cambium layer is therefore young wood, the outer young bark.

(6.) *Bark* (figs. 59, 60, 61, 62, 63, 64).—In early life the bark (*cortex*) is entirely cellular, like pith: but in a mature state it is composed of a cellular and a vascular system, in this respect agreeing with the wood; the arrangement is, however, reversed, for in the bark the cellular portion is outside and of great thickness, while the vascular is inside and comparatively small. These discrepancies did not, however, prevent Dutrochet calling the middle layer of the bark (the mesophlœum) the "cortical medulla." The four layers of the bark we accordingly find are all cellular, with the exception of the inner one or *liber*.

(*a*) This (figs. 62, 63) is often called the "bast layer," or *Endophlœum*,[2] and derives its more familiar name of *liber* from the fibrous layers of which it is composed separating in many cases

---

[1] *Cambio*, I change.

[2] Ἔνδον, within, and φλοιός, bark.

on account of the interposition of layers of cellular tissue, on maceration in water, into several leaf-like laminæ like the leaves of a book, or rather like the rolls of an ancient manuscript (figs. 60, 61). It does not, however, in all cases, form a continuous envelope, but it is broken up by the passage of the medullary rays into wedge-shaped divisions. It is composed of bundles of fibrous duct-like elongated cells, anastomosing among themselves, and forms a network the meshes of which are filled with cellular tissue. These fibrous bundles are formed of elongated cells, with very thick walls, and of small diameter, terminating in points or wedge-shaped extremities, and are known as *bast-cells* or *bast-tissue* (p. 40). According to Gray, complete and well-developed liber, like that of Basswood or Linden (*Tilia Europæa*), consists of three elements — viz. (1.) Bast cells or fibres; (2.) large and more or less elongated cells, with the inner walls variously marked with transparent spots, appearing like perforations, and usually traversed by an exceedingly minute network; and (3.) cells of parenchyma. On the inner layer are usually found some laticiferous vessels. The second-named element, which would appear to be the proper cells of the liber, as they are seldom or ever absent, contains an abundance of mucilage and proteine, and in all probability takes the principal part in the descending circulation of the plant — *i. e.*, in conveying downward and distributing the rich sap which has been elaborated in the foliage. The bast-cells are not essential to the liber, being altogether wanting in the bark of some trees and other plants. The liber grows by annual additions from the cambium, and it has frequently as many distinct layers as there are layers of wood, but in other cases there is not even a trace of such arrangement. In some plants, such as the vine and honeysuckle, the liber lives only one season, and is detached the following year, hanging "loose in papery layers or fibrous shreds." Towards the inner side of the liber, laticiferous vessels are often found, but tracheæ are markedly absent from every part of the bark.

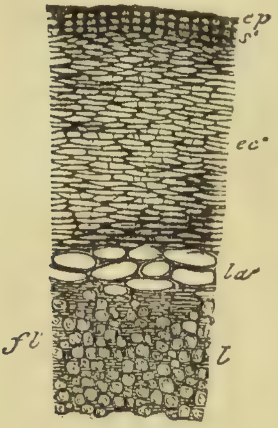


Fig. 64.—Transverse section (much magnified) of the very young bark of *Cinchona ovata*, intended to show the different layers which constitute the bark, before the progress of vegetation has modified it. *ep* Remains of the epidermis; *s* The suberous layer (in which the resinous matter is contained in the cinchonas); *cc'* The cellular layer (mesophlœum); *la* Lacunæ gorged with resinous matter; *l* Liber; *fl'* Cortical fibres (after Weddell, *Quinquinas*, Pl. II. fig. 42).

The liber of the lime-tree (*Tilia Europæa*) forms Russia matting; and that of the sack-tree of Coorg (*Antiaris saccidora*) is used to form mats, bags, &c. "Cuba bast" is the liber of *Paritium elatum* (order

Malvaceæ). In the lacebark-tree—*Laghetta linteria* (order *Daphnaceæ*)—it forms a somewhat regular network, on account of the medullary rays interrupting the straight course of the fibres. The toughness of the fibres makes them of economic importance. Thus the liber of *Linum usitatissimum* forms "flax," that of *Cannabis sativa* "hemp," that of *Bœhmeria nivea* (Hook. and Arn) the "China grass" of commerce—nearly all the members of the order to which it belongs (*Urticaceæ*) yielding fibre. The common nettle yields a strong fibre, which the North-West American Indians twist into string for making nets. In a word, the liber forms the main source of the fibres of commerce, no matter from what species of plants derived.[1]

(*b*) The *Mesophlœum*[2] (fig. 64), or green layer, is that layer of the bark immediately outside of the liber. It is distinguished from the liber by being cellular, and from the superimposed layers by the thin-walled globular or polyhedral cells, its greenish colour, and by the interspaces in it formed by the loose union of the cells. Richard has distinguished another layer between the mesophlœum and the epiphlœum under the name of *mesoderm* (the *collenchyma* of other authors), distinguished by being composed of cells rather elongated, unequal, thick-walled, and without green granulation in their interior—sometimes, as in *Acer pseudoplatanus*, the lilac, &c., forming a continuous layer, at other times showing a disposition to form into distinct bundles separated by the Mesophlœum. In general appearance, it may be remarked, the mesoderm resembles wax, and appears destined to moderate the superficial evaporation of liquids going through the stem when the epidermis acts feebly as a protector. According to Schacht, it is wanting in those stems where a layer of wax is developed in the epidermis of various large spurges—*e.g.*, in *Euphorbia canariensis*, *balsamifera*, and *piscatoria*. To apply a separate name to this structure is perhaps, however, in common with some of the names which Mohl has applied to structures in the bark, an over-refinement of nomenclature. The mesophlœum sometimes contains vessel-shaped lacunæ containing resin—*e.g.*, in pines, junipers, and various other coniferæ.

(*c*) The *Epiphlœum*,[3] or suberous layer,[4] has no chlorophyll in

---

[1] Between the liber and the mesophlœum—in fact, forming the outer part of the liber—is sometimes produced a layer of tubular cells, which, uniting to the mesophlœum, form those plates which detach from the bark of the "plane-tree" (*Acer pseudoplatanus*) yearly. To this layer Mohl has applied the names *Rytidom*, *internal periderm*, or *false liber*, and traces a correspondence between it and the external periderm (p. 92). In the plane this layer is not developed until the eighth year.

[2] Μέσος, middle, and φλοιός.

[3] Ἐπί, upon, and φλοιός. Sometimes the term *Exophlœum* (ἔξω, without, and φλοιός,) is used.

[4] *Stratum phlœum* of Hugo v. Mohl—*periderm* of Hanstein—a term which Mohl uses in a restricted sense.

the cellular tissue composing it. The cells are thin-walled, are placed close together, and are rectangular and elongated in a horizontal direction (figs. 60, 61, 64), being thus distinguished from those of the mesophlœum. It also is distinguished by remaining alive for a short time only, in wanting sap, and in its cells containing air. Its chemical characteristics are that, unlike cellulose in a pure state, it does not turn blue under the action of iodine and of sulphuric acid, even after being boiled in potash. It resists the action of sulphuric acid, which dissolves it when in a state of cellulose ; finally, by boiling in nitric acid, it gives suberic acid. According to Mitscherlich, cork is composed of 65.73 carbon, 8.33 hydrogen, 24.54 oxygen, 1.50 nitrogen ; while the cellular tissue of the tubercle of potatoes has the following composition: 62.3 carbon, 7.15 hydrogen, 27.57 oxygen, 3.03 nitrogen. It is often much developed, forming, in *Quercus Suber*, the well-known cork of commerce ; hence the name frequently applied to it—the *suberous* or *corky* layer. It is also largely developed in the bark of some other species of trees : for instance, on the stem of some *Aristolochiaceæ*, on the inferior portion of the stem of the curious Elephant's foot (*Testudinaria elephantipes*, Burch.), on the bark of a variety of elm (*Ulmus campestris*, L., var. *suberosa*), &c. When stripped off the cork-bearing tree, it can be renewed artificially by a process of growth which space will only permit us to describe very briefly. It appears that the cork of commerce is not a true example of this suberous layer, but is an artificial product. In this operation the first thing done is to pull off the natural bark of the cork-oak, known as the " male cork "—this operation being known to the Algerian colonists under the name of " le démasclage." The workman, in taking off the male cork, leaves on the trunk the mesophlœum and liber—these two layers being known to the colonist under the general name of " the mother." On a tree thus stripped, the cork of commerce (the " female cork " of the workmen) begins to form at a greater or less depth in the mesophlœum and in the liber. The "male," or natural bark, is close in texture, and not elastic ; while the female, or " artificial," is, as every one knows, very elastic, being composed of elastic porous cells.[1]

(*d*) The *Epidermis* is the outside skin which covers the bark. It is composed of flattened cells, in which wax is sometimes developed, giving it the familiar glistening appearance seen in many trees. It possesses stomata, scales, hairs, and other appendages, which we have already described (Sect. I.) On herbaceous plants, the epidermis remains unaltered ; but in perennial species it has to stretch to allow of the tree increasing in diameter, while in others it

---

[1] Casimir de Candolle—*De la Production naturelle et artificielle du liège.* Mém. de la Soc. de Phys. et d'Hist. Nat. de Genève, t. xvi.

cracks and falls off. The function of the epidermis then falls on the underlying epiphlœum, or rather of a particular portion—viz., what Mohl has called the *Periderm.* This is one or two rows of thickish-walled tubular cells, of a rather darker colour than the rest of the epiphlœum, and which mark the termination of each year's annual growth of cork. In plants in which the corky layer is feebly developed, this *periderm* is most marked; and it is to its coherent properties that the toughness of the bark of the canoe-birch (*Betula papyracea*, Wild.) is due. It is to this periderm, also, that is due the exfoliation in isolated plates of the bark of some trees, such as the planes, &c.

Variations in Structure of the Bark.—The bark is more varied in structure and growth than the wood; and, owing to distention by the growth of the wood, is liable to various abrasions and changes, as well as on account of its being exposed to all the influences of the elements without. Accordingly, in old trees it fissures and breaks off, so that its thickness in these trees never bears a regular proportion to the wood, even though the bark increases from within to the same annual amount as the wood. Hence a nail or other implement driven into the bark will, in due course, fall out; while, if put into the wood, it will get covered over by the annual increase.[1] The different layers grow by additions of cells to their inner face. The green layer does not grow at all after the first year; the opaque corky layer soon excludes it from the light, and it gradually perishes, never to be renewed. The corky layer commonly increases for a few years only by the formation of tubular cells.[2] In some trees, such as *Sequoia gigantea*, *Abies Douglasii*, the bark often attains a thickness of a foot or more. In others, by annual exfoliation, it is always about the same diameter.

Structure of the Stem of Annual Dicotyledons.—In annual dicotyledons the structure of the stem is the same in general as we have described in the preceding pages, but with the following differences: (1.) The bark is more simple in its structure, and the bundles forming the liber present these modifications,—(*a*) they form a continuous layer; (*b*) they are isolated and distinct in the middle of a herbaceous envelope; (*c*) they are placed immediately under the epidermis. (2.) The medullary rays are in general larger than in perennial plants.

---

[1] Numerous such instances are on record, or continually being recorded in the journals of the day.—*Vide* several such in Histoire de l'Academie des Sciences, 177, cited in Bocquillon's La Vie des Plantes, 150. In some trees, which naturally branch from near the base, if growing in a dense forest or thicket where light cannot penetrate to the lower branches, these branches will often drop off at an early stage, and the scars left by their attachment get grown over by the bark, so that no visible trace remains to show that the trees were not originally unbranched from the trunk.

[2] Gray, l. c.

The Uses of the Stem will be duly considered when the function of nutrition comes to be discussed. In the mean time, dogmatically and in a few words, the functions of the various parts may be summed up as follows: (1.) The *pith* supplies nourishment to the young plant; (2.) the *medullary sheath* keeps up the connection between the leaves and cortical parts of the stem by means of the spiral vessels which can be traced into the petiole of the leaf, and seem intended for the conveyance of air; (3.) the *medullary rays* keep up a connection between the pith and the bark, and possibly help to produce leaf-buds; (4.) the *cambium* forms the wood and bark; (5.) the *bark* protects the tender wood, conveys the sap downward from the leaves after being elaborated, and contains many useful products (gum, tannin, turpentine); (6.) the *woody portion* conveys sap from the roots to the leaves—at one time all did this, but latterly only the open vessels, all the rest having got filled up by woody matter.

STEM OF MONOCOTYLEDONS.

To this type belong the stems of the palm-trees of tropical and subtropical countries, as well as many other trees and shrubs of those countries, and though in the north all of the arborescent species belong to the preceding class, we have many humble representatives of the Monocotyledonous, Endogenous, or inside growers. The palms may, however, be now conveniently taken as the representatives of this class of stems; their habit of growth — growing unbranched to the height of from 20 to 150 feet, with umbrella-like crowns of leaves—giving a striking aspect to the scenery of the countries they are found in (fig. 67).

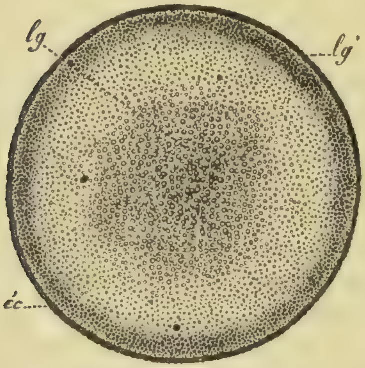


Fig. 65.—Transverse section of the stem of a palm. *éc* Cortical zone; *lg* Internal portion, with woody bundles comparatively few, and not crowded together; *lg'* Peripheral portion of the wood to which the numerous firm fibro-vascular bundles give considerable hardness.

Structure.—The structure of the stem is widely different from that of dicotyledons (fig. 65). Instead of showing pith, concentric circles of wood, and a detachable bark with the intervening cambium layer, we find the woody bundles scattered irregularly through the stem from within outward; the pith, as found in the dicotyledon, is absent; there is no cambium layer; and the bark can with difficulty be detached from the wood.

Examining the structure of this kind of stem more minutely, we find that it is composed of woody bundles, or vascular fibres, scattered in the midst of cellular tissue, of which the greater mass of it is composed, without any appearance of superimposed layers.

The woody mass of the stem is composed of thickened cellular tissue, in which the vascular bundles already mentioned are scattered, the one distinct from the other, but more numerous, closer together, and harder towards the exterior than towards the interior of the stem, contrary to what we find in dicotyledons.

There is no medullary canal and no medullary rays.

Each vascular bundle is composed of (1) spiral vessels, (2) fibrous vessels, (3) proper or laticiferous vessels, (4) cellular tissue. 1. The spiral vessels (tracheæ, or punctated vessels) occupy in general the centre of each bundle. 2. The laticiferous vessels are placed outside the spiral vessels. 3. The fibrous vessels are ordinarily in two bundles,—the one external, which may be considered, according to Mohl, as corresponding to the liber of the dicotyledonous bark; the other internal, placed on the interior side of the spiral vessel, may be compared to the woody body of the same stem. The cambium disappears after each bundle has completed its growth or become "definite;" but it is present in the young state.

The *bark* is composed of (1) an epidermis, (2) cellular tissue, (3) bundles of fibrous vessels, which are sometimes wanting, but never forming, as in the liber of dicotyledons, leaf-like layers.

In general, authors have described monocotyledons as having no true bark; and it is to Richard[1] that we are indebted for showing the erroneousness of that idea. Schacht has even described the cambium layer as existing in the stipe of *Dracæna*. In various palms and in grasses the bark is covered with a hard epidermis containing silicates. In various palms — *Caladium*, *Phœnix*, *Chamædorea*, *Sabal*, *Raphis*, &c.—we find, on the inside of the bark, bundles of fibrous tubes, isolated, but forming a somewhat regular ring.

The vascular bundles get indurated, by the deposition of lignine, in course of time.

Their direction in the interior of the stem is always about the same. They may be usually traced from the base of the leaves down through the stem, "some of them to the roots in a young plant, while others, curving outward, lose themselves in the bark." As new leaves are developed, new fibres descend into the interior of the trunk, and then, after descending so far, curve outwards towards the bark, with which they get incorporated, thus accounting for the difficulty with which the bark is detached from the

---

[1] Nouv. Elém. de bot., 7e éd. p. 132.

stem. This method of increase from within outwards will go on as often as new leaves are developed, until the bark will no longer distend, when the growth ceases (fig. 66).

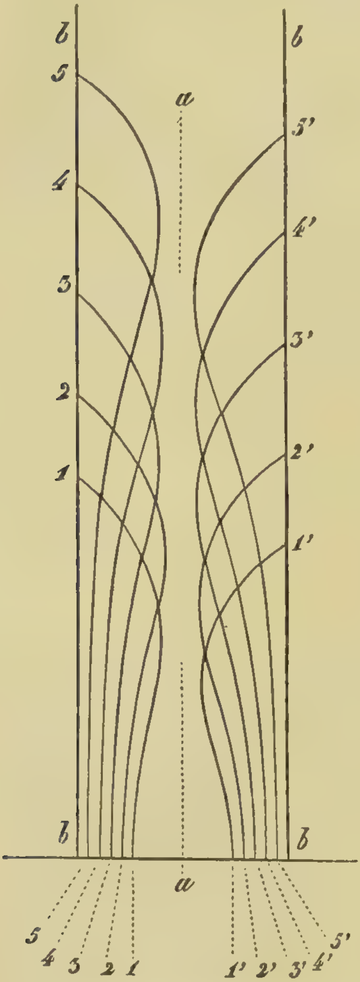


Fig. 66.—Diagram intended to show the course of the fibro-vascular bundles in the stem of a monocotyledon. *b b-b b* Indicate the size of the stem ; *a a* Its median line. The bundles to the left, 1 2 3 4 5, and those to the right, 1' 2' 3' 4' 5', point to the leaves, newer or older, according to the same order of the numbers.

In *Dracæna*, however, the bark remains soft through life. Hence some trees of this genus—for example, the gigantic dragon-tree of Teneriffe, which, at the time of its death, was about twelve feet in diameter ten feet from the ground—will attain great dimensions. The bundles, however, through their whole length, have not the same organisation. At their inferior extremity they are smaller in diameter, and are composed of fibrous tubes; higher up they show laticiferous vessels, then spiral vessels; still higher the false spiral vessels; and lastly the true spiral vessels.

From what we have said, it will be seen that the woody mass in the centre of the stem is the newest and the softest (hence sometimes called the "pith"), and the part outside the oldest and hardest. The wood of the lower part of the stem and the rind is also firm, from the greater number of woody fibres which terminate in them, and also from its proper induration in the former case.

Growth of Palms.—Palms usually grow from a terminal bud alone. Accordingly, if this bud is destroyed, the tree dies. However, on the Doum palm (*Hyphæne Thebaica*) of Egypt, and the *Pandanus* or screw-pine (belonging to the order *Pandanaceæ*, near allies of the palms), two or more buds are developed, which give rise to two or more trunks and branches; and when, as in the asparagus, lateral buds are developed, or, as in the bamboo, maize, &c., leaves are scattered along the stem and branches, these latter taper, just as in dicotyledons; while in the case of the Doum palm, &c., the branches are cylindrical like the stem.

Theoretical Structure of the Stem of Monocotyledons.—Comparing the structure of an *exogenous* with an *endogenous* stem (to use the terms suggested by their structure), we find that in the first the woody part consists of wedges of wood composed of layers formed by the inside cells of the cambium year after year, as long as the life of the plant extends, these wedges being separated one from the other by the interposition of the cellular medullary rays. In the endogenous stem we find no such arrangement of concentric circles of wood forming wedges with the sharp end next the pith and the broad end next the cambium and liber. Neither exist. However, the two stems, if we examine them closely in a philosophical spirit, will be found not to be so entirely different from each other as might at first sight be imagined. An analogy can be traced between the parts of each. Each thread or fibrous bundle in the endogenous stem has all the elements found in the stem of the Exogen, though sometimes irregularly mixed. This we have already hinted at. A section of one of these threads shows

Fig. 67.—*Metroxylon Rumphii*, one of the palms from the central portion of the stem of which sago is extracted in Malacca; *a*, *b* Fruit whole and in section.

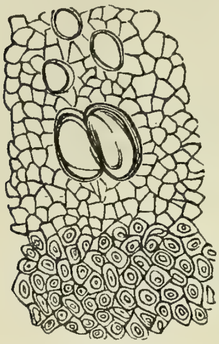


Fig. 68.—Section of a woody bundle from an endogenous stem (a palm). Outside are thickened walled fibres, considered to be liberian. Immersed in a mass of parenchyma are seen the mouths of two large dotted vessels, while the three smaller openings are the mouths of spiral vessels. In the figure the laticiferous vessels do not appear; they are usually immediately within the liber, like outer fibres.

woody fibre, and one or two spiral vessels on its inner border, corresponding to true wood; and the thick-walled elongated cells on its outer border have been shown by Mohl[1]—who originally pointed out these correspondences—to be of the same nature as the bast-cells of Exogens. "Between the two is a structure of parenchymatous cells mixed with elongated and punctated cells, answering to the proper cells of the inner part of the liber. The portion of each endogenous thread, therefore, which looks towards the centre of the trunk, answers to the wood, and its outer portion to the liber, or inner bark of the exogenous stem; and the parenchyma through which the threads are interspersed answers to the medullary rays and pith together. The main difference between the endogenous woody threads and the exogenous woody wedges is, that there is no cambium layer in the former between the liber and the wood, and therefore no provision for increase in diameter. The bundles are therefore strictly limited, while those of Exogens are unlimited in growth. In Exogens the woody bundles or wedges, symmetrically arranged in a circle, become confluent in a zone in all woody and most herbaceous stems, which continue to increase in thickness. In Endogens the woody bundles are unchanged in size after their formation; but new and distinct ones are formed in the growing stem with each leaf it develops, and interspersed more or less irregularly among the older bundles"[2] (fig. 67).

STEM OF ACOTYLEDONS.

The *stipe*, *caudex*, or *rachis* of Acotyledonous plants, like ferns, &c., forms the type of stem which has been called the *Acrogenous* or summit grower. It differs from both the Dicotyledonous and Monocotyledonous stems in having neither concentric circles

---

[1] Martius' Palmæ (Intro.), 1824. His doctrine has been opposed by Mirbel, Gaudichaud, and others, but still holds its ground.

[2] Regarding the theory of stem-formations generally, Schleiden holds some very peculiar ideas, which those interested in the views of that botanist can find in his paper, "Über die Anatomisch-physiologischen Verschiedeiherten der Stengelgebilde," in Wiegmann's Archiv., 1839, p. 219; or in various English abstracts which the admirers of that style of botany have taken the trouble to make. They are not, I believe, usually given in modern text-books.

of woody matter nor woody bundles, being simply formed by the base of the leaves. In a tree-fern, for instance, the leaves form a crown on the summit as in the palm. New leaves are formed year after year, one circle within those of the former year, which have died away, leaving their bases to increase the diameter of the stem, which therefore decreases from the base upwards. Examining its structure more intimately, we find that it is composed somewhat differently in the various acotyledonous orders, though the first we shall speak of may be taken as the type of them all.

Ferns.—The woody stem is composed for the most part of cellular tissue and vascular bundles. The structure is best studied on a tree-fern, some of which reach 60 or 70 feet in height. On examining one of these, we find the external surface marked by the scars where leaves have been attached, and in these scars dots showing the openings of fibro-vascular bundles. This external portion is a kind of bark, very dark brown and thin, but in which it is possible — according to Mohl[1] — to distinguish two concentric layers, the exterior of which is composed of polyhedric parenchyma, while the interior has no elongated cells or prosenchyma. Within this bark, and separated from it by a thin zone of parenchyma, is seen a circle of large fibro-vascular bundles, unequal in size, and looking, on transverse section, each like a twisted band, single or double, with the corners outwards. These bundles are produced, not gradually, but simultaneously—being continuous with the vessels in the leaves. The vascular bundles are grouped and reunited in such a manner that they form very dark-coloured bands, stretching the whole length of the stipe, differently shaped in different species, but with a kind of regularity or symmetry in the same species. These vascular bands, in uniting, form the woody mass of the exterior of the stem. The interior, occupied by cellular tissue, is somewhat white. All the bands are fastened together through the whole length, except in one or two points. These bands ordinarily are united in twos, leaving between them a space filled with cellular tissue—giving to the transverse section of stem that peculiar figure-like marking which in the ordinary *Pteris aquilina* (bracken) has been compared to a two-headed eagle. They are formed of woody tissue, in which the fibrous tubes have thin walls, and are coloured by a brown substance. The tissue placed between these black perpendicular bands is composed of—(1.) scalariform vessels, very numerous, ended by cells short and very regular; (2.) of true vessels or cells, very long, unequal, and thin-walled.

The whole parenchymatous mass is formed of cellular tissue. It is thus seen that the stem of ferns differs from that of monocoty-

---

[1] Martius' Icones plantarum Cryptogamicarum Brasiliæ, 1833.

ledons in (1.) the woody bundles being less numerous, or by the form of the longitudinal bands; (2.) by the woody bundles in the fern anastomosing among themselves, so as to form a sort of sheath, which is not seen in the monocotyledons; (3.) by the ferns never containing in their adult state true spiral vessels. Of late years, however, Bert[1] has shown that in ferns in a very young state these vessels are found, though they soon disappear, to give place to the scalariform vessels so characteristic of the order. In some of the larger species of tree-ferns adventitious roots come out, and in reaching the ground swell out the inferior portion of the stipe. They also have the power of growing for a long time in the direction of their length, the other parts not taking any share in the increase.

Equisetaceæ.—In the "horse-tails," or Equisetaceæ, the aerial stem is annual, cylindrical, and hollow, though divided by partitions corresponding with the nodes where the branches are given off. The vascular system of the stem consists of a cylinder of distinct, very regular bundles, composed of annular or spiral vessels. The most internal of the vessels of each of these bundles have become absorbed,[2] and in their place are regular and constant lacunæ, which accompany towards the interior each of these bundles in the adult plant. The whole is surrounded by an epidermis, often hard from the deposition of silicious matter, and furnished with lines of stomata. This temporary existence of vessels to subserve a temporary purpose has been also noticed by Chatin and others in aquatic plants. The flinty matter in the epidermis—which has caused these plants to be used in commerce as polishing materials, and to have received the name of "Dutch rushes," on account of the Dutch housewives from time immemorial having used them to polish brasses—is considered by Douval-Jouve as a secretion of the external cells of the epidermis in contact with the air, and not as entering into even the constitution of their membranes.

Lycopodiaceæ.—The stems of Club-mosses present an organisation rather peculiar. The centre is occupied by a woody axis, composed of scalariform vessels analogous to those of ferns, and surrounded by a cellular zone, through which adventitious roots make their way outside, often extending to a great distance.[3] It may, however, be noted, that in *Psilotum triquetrum* the vascular bundle is not all in the centre, but surrounds a mass of cellular tissue analogous to the pith. The structure of Lycopodiaceæ is im-

---

[1] Bert, Bull. de la Soc. Phil., 1859, p. 26; see also Mettenius, Über d. Bau von Angeopteris, in Memoirs of the Royal Academy of Saxony, vi. (1863) 501-570.

[2] Douval-Jouve, Histoire naturelle des Equisetum de France, 1864.

[3] Brongniart in Archives du Muséum, i. pl. 32.

portant in so far as they appear to be the true living representatives of the extinct gigantic *Lepidodendrons* of the Carboniferous era, which present, notwithstanding attempts have been lately made to prove that they are of a unique structure—exogenous among vascular cryptogams—a perfectly similar structure. In *Lycopodium* *Chamœparinus*, there is a cylinder of wood-cells surrounding the central cylinder of united fibro-vascular bundles. This cylinder of wood-cells represents, and is a mere modification of, the cellular tissue met with in the ordinary stems of lycopods. The central portion is not a pith, though analogous to it, but consists of the central group of the fibro-vascular bundles, and is not the homologue of the woody cylinder in Exogens.[1]

Fig. 69.—*Lycopodium clavatum*, L., the common club-moss, with (*a*, *b*) the fruit (conceptacles) magnified.

In addition to the peculiarity of the structure of the stems in *Lycopodiaceæ*, there is a further peculiarity in their mode of elongation. Instead of terminating in one, they terminate in two collateral buds; so that, deprived of axillary buds, they lengthen by a curious dichotomous ramification (fig. 69).

---

[1] See Sach's Lehrbuch (1873), s. 100, 107, &c.; W. R. M'Nab, Nature, Aug. 31, 1871 (with the discussion by Williamson, Dyer, and others in subsequent numbers); and the papers of Williamson in the Phil. Trans., 1871; and M'Nab, Trans. Bot. Soc., 1872-73.

Ferns, Club-mosses, and Equisetaceæ are the only Acotyledonous or Cryptogamic plants which have true stems with vascular tissue, and hence they are called the vascular cryptogams. All the others—Algæ, Mosses, Lichens—are cellular, and have no true stems.

SUBTERRANEAN STEMS.

Hitherto we have only spoken of aerial stems, which grow above ground, and are familiarly known as such. There is, however, a large and interesting class of stems which are concealed underground, and commonly classed as roots. Sometimes this subterranean stem is the only one which the plant possesses; at other times both an aerial and a subterranean stem are found on the same plant. They are distinguished from roots by producing regular buds, or "by being marked with scars which indicate the former insertion of leaves, or furnished with scales which are the rudiments or vestiges of leaves." In older botanical works, they may be usually found classed as roots; and all the *scaly roots* of these writers are stems of this nature. What are commonly called *Creeping roots* are equally included in the underground stems of the botanist. In structure they do not materially differ from the aerial stems. The medullary canal is, however, frequently absent in the underground stem of Dicotyledons. In like manner the underground stems of Monocotyledons do not differ in structure from the aerial one. The presence of unrollable tracheæ distinguishes it from that of the former class. Let us consider a few of the principal forms of these.

Rhizome, or Rootstock, is a general term applied to "perennial, horizontally elongated, more or less subterranean root-like forms of the stem, and more particularly to those which are considerably thickened by the accumulation of starch, or other forms of nutritive matter in their tissue." Examples are found in the Ginger, Iris, Calamus (fig. 70), and the ordinary underground "root" of the fern, which has two forms of stem, the aerial and the subterranean. They grow and branch in the same manner that ordinary stems do, and emit the true roots from the under side of their whole surface. In "Solomon's seal" (*Polygonatum*), the place where the last year's growth has terminated and the next year's commenced is marked by a circular scar shaped like a seal, hence the name; and in the rhizomes of other plants by a contraction which gives the rhizome a somewhat knobbed appearance. The rhizome can be distinguished from the true root by the presence of one or more buds or scales. Rhizomes may be divided into two categories—viz., *Indeterminate Rhizomes*, when the stem is terminated by a bud destined to prolong it directly (Ex. *Butomus umbellatus*, *Triticum repens*, couch-grass,

&c.); and *Determinate Rhizomes*, which, instead of the terminal bud, have lateral buds, as in the axil of a leaf, from which each year a branch issues (Ex. *Polygonatum multiflorum*, and the greater number of underground stems of the rhizome type). It is also sometimes called a *Sympodium*.[1]

Sobol.—This term is frequently applied to an underground stem, which, like the *Couch-grass*, *Carex arenaria*, &c., sends roots from one part and leaf-buds from another. Creeping stems of this nature are useful in binding together drifting sands, and thereby preventing them drifting.

Fig. 70.—*Calamus aromaticus*, showing the rhizome (*a*).

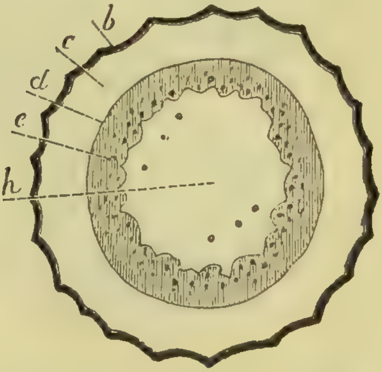


Fig. 71.—Transverse section (magnified) of the rhizome of a *Smilax* (order *Smilaceæ*), which yields the Brazilian sarsaparilla. *b* Bark; *c* Outside harder portion of wood; *d* Interior portion, with *e*, woody bundles through it; *h* Soft disrupted internal portion corresponding to the pith of dicotyledons.

Tuber.—A "tuber" is that form of subterranean stem seen in the Jerusalem artichoke (*Helianthus tuberosus*), and the ordinary

---

[1] For an exhaustive account of rhizomes, &c., see Thilo Irmisch, Zur morphologie d. Monok. Knollen-u. Zwiebelgewæchse, 1850; Clos in Ann. des. Sc. Nat., 1850, t. xiii.; Fabre, ibid., 1855, t. iii.; Duch. l. c.; and Turpin's Mems. (l. c.)

potato (*Solanum tuberosum*). It is usually caused by the enlargement of the growing bud of a subterranean branch, and the deposition of starch, &c., in its tissue (Gray), which deposit serves for the nutrition of the buds (eyes) which it evolves when they develop in the following year, corresponding in this respect somewhat to the bulbous roots of the turnip, &c. In other words, it is a stem with very much shortened internodes. In the

Fig. 72 —Young plant of the potato (*Solanum tuberosum*) raised from seed. *r r* Root axis ; *c* Neck ; *ct ct* The two cotyledons expanded into little germinal leaves—in their axils are two branches, swollen at their extremities into tubercles *tb tb ; éc* Little leaves or scales of the subterranean branches ; *éc'* Scales of the tubercles, in the axes of which the buds *br* are found ; *b b* Branches equally subterraneous and tuberiferous arising from the axils of the inferior leaves ; *b'* A ramification of one of these ; *r'r'* Adventitious roots arising from the same branches ; *f'* Extremity of one of the branches, which, accidentally growing into the air, produces a tuft of leaves instead of a tuber; *f f f* Ordinary leaves situated on the part of the stem out of the earth (reduced after Turpin[1]).

---

[1] Mém. sur l'organisation intérieure et extérieure de tubercules du *Solanum tuberosum*, &c.—Mém. du Museum, xix. (1830) 1-36, pl. I-V.

familiar example of the potato, we have a green leaf-bearing aerial stem, and an underground not green, and bearing leaves, if any,

Fig. 73.—Tuber of potato which has grown out of the soil, and is prolonged upwards in a leafy stem *t*; at *a a* we see the depressions on which the buds are fixed; at *a'* buds already developed into little leafy shoots.

only in the form of scales. The buds which are present, however, in the form of "eyes," give rise to branches, which rise above ground, and bear leaves, flowers, and fruit. The stunted underground stem constitutes the "potato" of culinary fame. Sometimes, however, under certain circumstances of light and nourishment, the aerial stem, instead of giving form to the ordinary branches, will bear tubers. The nature of these tubers is shown in the very instructive figures[1] (71, 72) taken from actual

---

[1] See also Gardeners' Chronicle, ii. 85, where such another specimen is figured and described.

specimens. Between the ordinary rhizome and the tuber there are various gradations in the form of such tuber-like masses, formed, as in the case of the *Cyclamen* cultivated in our gardens, by a swelling, owing to the increase of cellular tissue in the lower portion of the stem, and in the case of the carrot, radish, &c., by a similar enlargement of the root proper. Finally, in others, as the beet (*Beta vulgaris*, L., var. *rapacea*), we see that the stem and the root both take part in this swelling, forming tuberoid masses. In the mass commonly called "a beet," M. Decaisne recognises two parts usually confounded together, — viz., an inferior portion, made up of the root; and a superior, formed by the part comprised between the base of the root and the attachment of the cotyledons (the "hypocotyle" of some authors). The last portion is generally out of the ground, while the first is fixed in it. The pith, which occupies the centre of the first in the form of an inverted cone, is surrounded by a medullary sheath with spiral vessels—wanting in the second, or at least existing only with reticulated vessels: lastly, the nitrogenous materials are chiefly found in the first portion, where at the same time a great number of little rhomboidal crystals are seen; while the second, or stem portion of the beet, is particularly characterised by its richness in sugar.[1] These facts, the reader can easily see, have an important practical bearing on the cultivation of beet.[2]

Corm.—We see this in *Colchicum*, *Crocus*, Cuckoo-pint *(Arum maculatum)*, Snowdrop *(Galanthus)*, Gladiolus, &c. It differs from the bulb in being solid, and from the tuber by its rounded oval figure. Shortly, it may be described as a bulb in which the scales are all solidified into one mass. It is usually the thickened end of the stem, and may bear leaf-buds at the summit or side, and may be regarded as "a much-shortened rhizome, consisting of a few undeveloped internodes."

TERRESTRIO-AERIAL STEMS.

There is another class of stems which, while perhaps more aerial than terrestrial, partakes somewhat of both characters. These are the stems which creep along the ground. They have received various names, according to their character.

Stolon (offset or hybernaculum).—When a stem naturally falls to the ground, and, when favoured by light and shade, takes root,

---

[1] Duchartre, Eléments, p. 267.

[2] Tubercular structures, according to the theoretical ideas of the authors treating them, have been divided into various groups. Clos gives, for instance, eight kinds (Ann. Sc. Nat., 1850); but the student will find the above quite sufficient for his purpose, without further complicating it by details.

and, ascending, forms an ordinary aerial stem capable of extracting moisture from the soil through means of the adventitious roots which it has given out, it is called a "stolon." Such a stolon can be separated from the mother plant, and lead an independent existence, as the gardener is well aware when he grows the currant, gooseberry, &c., in this way, which he calls "layering."

Sucker (surculus).—The Rose, Raspberry, Asparagus, and Mint afford examples of this kind of stem. After running along the ground and emitting roots, it will rise into an ordinary aerial stem. When these branches or stems grow rapidly they are often called *shoots*. The gardener takes advantage of this tendency by cutting off the sucker's connection with the mother plant, and propagating it by "division" or "parting the roots."

Runner is much the same as a sucker, only, instead of the stem taking root at various portions of its course, the runner is a slender branch given off from the base of the plant, which, taking root, gives rise to a tuft of leaves, and if divided from the parent can give rise to an independent plant. The strawberry (fig. 74) is an example of this. When, as in the case of the house-leek, a shoot presents a branch with a tuft of leaves at the end, which takes root while resting on the ground, it is called an *offset*. These offsets afterwards become independent plants.

Fig. 74.—A strawberry plant (*Fragaria vesca*, L., var. *semperflorens*) out of flower, showing the runner rooting, and giving origin to tufts of leaves at two successive nodes.

Bulbs.—A bulb is usually defined as "a permanently abbreviated stem, mostly shorter than broad, and clothed with scales which are imperfect thickened leaves, or more commonly the thickened and persistent bases of ordinary leaves." It may be distinguished into three parts: (1.) the stem which develops upwards, bearing stalk, foliage, flowers, and fruit; (2.) inferiorly, the true roots or radicles; and (3.) the bud, in the shape of scales, in which nutritive matter is stored up (fig. 76). Of this form the hyacinth and onion are at once the most familiar and best examples. What is commonly thought to be the root of the hyacinth is in reality the "underground stem;" and the true roots may be seen depending from it in the earth or in the water (when so grown) in the shape of the radicles from its inferior surface. A bulb is, however, in reality a fleshy permanent bud, usually underground, the scales being modified leaves; and the real stem, morphologi-

Fig. 75. — Longitudinal section of the lower portion of an onion plant in flower. *bl* Bulb showing the different "scaly" layers or tunics; *r* Base of the bulb; *t* Flowering stem, of which the swollen portion commences at *a*; *f'* Lower leaf, almost reduced to its sheathing portion (vagina); *ff* The other leaves divided longitudinally, so as to show their interior cavity.

Fig. 76.—Scaly bulb of the white lily (*Lilium candidum*), with the tuft of leaves which it produces. *bl* The bulb itself; *éc* Scales which it forms; *pl* The bottom of the bulb (not seen in the figure); *f* Leaves with well-developed blades; *r* Roots depending from the base of the bulb (⅓ nat. size).

cally considered, is the central cone, from the base of which the roots are attached. An examination of fig. 75 shows that the bulb-scales are a continuation of the leaves, and in fact are simply the expanded base of the petiole.

Bulbs, like rhizomes proper, may be divided into two series—*determinate* and *indeterminate.* The first, like the onion and dahlia, vegetates, and gives origin to thin flowering stalks from its vegetative extremity, and accordingly perishes after once flowering; while the indeterminate bulbs, of which the hyacinth, amaryllis, and many others, are examples, flower by the development of lateral buds in the axil of their scales, below the summit of the axis,—in each year the terminal bud, always living, is able to produce new leaves and to continue the axis; while, on the other hand, new lateral buds are produced, and give forth new flowering branches. Hence such *indeterminate bulbs can live an indefinite number of years.*[1]

Bulblets are small bulbs produced in the axils of the leaves of several plants, which fall, take root, and develop into a plant exactly the counterpart of that which produced it. Such plants are called *viviparous.* Examples are afforded by the *Lilium bulbiferum*, *Allium carinatum*, *Dioscorea batatas*, *D. bulbifera*, &c., where they are often produced in the place of flower-buds —showing plainly the identity of bulbs with buds. Of a similar character are the little buds produced at the extremities of the branches of some aquatic plants—*e.g.*, *Aldrovandra vesiculosa*, *Sagittaria*, &c.—which, during winter, fall to the bottom of the water—weighed down by the starch with which they are charged —and, taking root in the mud, rise to the surface in spring in the form of a new plant. Some such aquatic plants, rarely producing seed, propagate themselves entirely in this manner. Properly speaking, all the forms of bulbs and bulblets ought to have been included under the head of buds, though, for the sake of convenience, we have considered them while describing the allied terrestrio-aerial stems.[2]

The Uses of Bulbs to man are rather extensive. Among those used for food, or as condiments, may be mentioned the common onion (*Allium cepa*, L.), garlic (*A. sativum*, L.), shallot (*A. ascalonicum*, L.), scallion (*A. fistulosum*, L.), chive (*A. schœnoprasum*, L.), leek (*A. porrum*, L.), rocambole (*A. ophioscorodon*, Don), &c.; while the Indians of North-West America use the bulbs of the blue-flowered *Camassia esculentea* (Lind.) as winter stores of

---

[1] Duchartre, Eléments, p. 417.

[2] The word *scape*, which the older botanists apply to the flower-bearing axis of a bulbous plant, provided it was deprived of leaves, had better be dropped out of use, since there exists every possible transition form between the axes which bear only flowers and those which bear leaves.

food;[1] while *Lilium tigrinum*, Gawl., *L. Thunbergianum*, Rœm. et Schult., and *L. Camschatkense*, L., are cultivated in the countries in which they are native as articles of diet.

SPINES, TENDRILS, ETC.

Spines.—These must be classed as arrested or modified branches, differing from the thorns of the rose or other plants in being connected with the wood and not with the epidermis, and accordingly cannot be detached except by tearing the substance of the stem. They can further be proved to be branches by the fact that frequently (as in the hawthorn) they bear leaves and buds like true branches, and by their being placed in the axils of the leaves. Moreover, they show every gradation between a true branch and a pointed indurated spine. Sometimes, as in the *Acacia*, the *Echinopanax* or prickly ash of America, &c., the stipules are developed into spines. In *Astragalus tragacantha* and *Volkameria aculeata*, the persistent petioles get so altered; and, as in *Asparagus horridus* of Africa, and the Barberry even, the leaf itself gets so transformed. When the spine springs, however, from the axil of a leaf, it must be looked on as a branch. In some plants, as in the Honey-locust (*Gleditschia*), the spines branch in a very complicated manner. Sometimes the spine will grow into a true branch if the bush or tree on which it grows is transplanted to good soil (*e.g.*, in the sloe), or cultivated for some time. According to their situation spines are, in descriptive language, *caulinary* when on the stem (*Cactus*, *Gleditschia*); *terminal* when at the extremities of the branches (*Prunus spinosa*); *axillary* when in the axils of the leaves (*Citrus medica*); *infra-axillary* (common gooseberry, *Ribes grossularia*), &c. These, and the terms *simple*, *branched*, *solitary*, and *fasciculated*, explain themselves.

Tendrils sometimes belong to leaves, as in the Pea, where they are prolongations of the leaf-stalk or midrib; but they are more commonly "thread-like leafless branches, capable of coiling spirally," in order to attach climbing-plants to other bodies for support. Some tendrils *hook* their tips round supporting objects, while others expand their tips into a flat disc, which clings to objects, and so enables the plant to climb up in much the same way as do the accessory rootlets of *Ampelopsis*, the Virginian creeper.

---

[1] I have given a full account of this in "Plants used by the North-West American Indians in Food, Medicine, and Domestic Economy."—Trans. Bot. Soc. Edin., vol. ix.

ANOMALOUS STEMS.

Exogenous Stems.—Hitherto we have only spoken of the structure of the three great classes of stems as normally found in three great classes of plants. It has, however, been mentioned, when speaking of the formation of annual rings of wood in Dicotyledons, that in countries where there is no sensible interruption of the growth of vegetation, the stem may show no mark of each year's growth, as in the ordinary concentric layers of wood of the Exogenous stem.

There are also known to exist various anomalous kinds of stem, chiefly *lianas* or twining plants, which, while in no way altering the great facts already mentioned, deserve notice.

Cycadaceæ.—In these plants one annual layer of wood is not formed every year, but it takes several years to form one. Accordingly, even in old plants there are very few rings. The zones of wood are separated by a layer of cellular tissue, like that of the pith, and often as thick as the zones themselves, while the pith is filled with bundles of fibro-vascular tissue.[1]

Coniferæ.—The stems of this great order are, like those of Cycads, distinguished from those of ordinary dicotyledons by the absence of ducts proper in the woody layers, and by the large areolar discs on the walls of the wood-cells, already noted as being present on the wood of trees of this order (p. 39). The wood of the yew (p. 39) and the Douglas fir (*Abies Douglasii*) form exceptions to this structure. It also sometimes happens in firs that the wood is produced in an oblique instead of a perpendicular manner — a peculiarity said to be inherited by seedlings from such malformed trees.

Gnetaceæ. — In this order (which is closely allied to the Coniferæ), of which one of the most remarkable plants is *Welwitschia mirabilis*, Hook. f., discovered in Africa, the woody layers of plants in the section *Thoa* are separated from each other by the interposition of thin layers of liber. In fig. 77, another anomaly, in a Gnetum, copied from a specimen in the collection of the Faculty of Science in Paris, is given.

Fig. 77. — Fragment of the stem of a *Gnetum*, in which one branch originating at *a*, takes a spiral turn or two around the stem, to be again incorporated with it at the point *b* (1-6th nat. size).

---

[1] Brongniart in Ann. des Sc. Nat., ser. 1, xvi. 389, t. 20, 21; Link, in Ausgew. Abbild. 2. t. i.; Mohl in Abhandl. Akad. Munich, 1832, and in Verm. Schrift. 195; Miguel, "Stamm. der Cycas" in Linnea, 1844, (xviii.) 125, or Ann. Sc. Nat., ser. 3, v. 11.

Sapindaceæ.—This is a tropical order having many plants, which twine themselves around other trees (*lianas*),[1] and the stems of which are often angular instead of being round. On transverse section, we see that the stem is in reality made up of several smaller stems united into one solid mass, and surrounding a central stem. This central stem is formed of woody layers, in general not very distinct one from the other, but showing a medullary canal and medullary rays. Each of the smaller stems or woody bundles has in general an excentric medullary canal (figs. 78, 79), in some cases even with an imperfect medullary sheath; but this, it ought to be mentioned, is denied by Naegli, who has made these stems a subject of study. Until recently, it was believed that these secondary or tertiary woody growths on the outside of the main stem were simply branches which had twined themselves around it, and got incorporated therewith. The recent observations, however, of Señhor Netto, a Brazilian botanist, show that neither this explanation nor that of Naegli—that in the Sapindaceæ the cambium is not formed all around at once, and in consequence leaves outside of it certain portions which become the origin of the exterior woody bodies—will account for all the anomalies of structure we find in the Sapindaceæ. There seem in reality to be separate foci of development in some of the stems, and in others—but more rarely—a sort of process of dismemberment which operates on the primitive homogeneous woody mass.

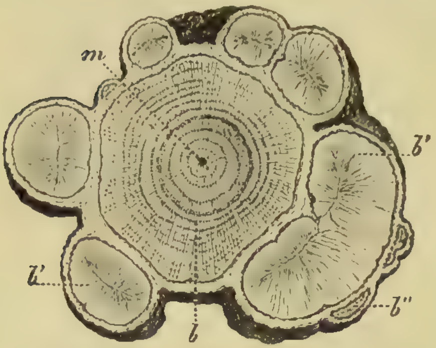


Fig. 78.—Transverse section of a stem of a twiner ("liana") of the order Sapindaceæ (perhaps *Serjania Dombeyana?*). Here we see, 1st, A primary or central woody mass *b*, with the pith *m* in its centre; 2d, A circle of secondary woody bodies (*b' b'*), very unequal in size; 3d, Two little tertiary woody bodies *b''*, placed in a third still more exterior circle, of which they are the commencement.

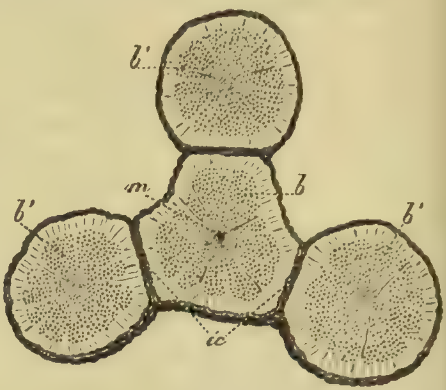


Fig. 79.—Transverse section of a liana of the family of Sapindaceæ (perhaps *Serjania cuspidata?*). Here we see, 1st, A central woody body *b*, with a central pith *m*, and an envelope of bark *éc*; 2d, Three secondary woody bodies *b' b' b'*, without pith, but equally surrounded by a thick layer of bark.

---

[1] *Lianas* of the Spaniards; *lianes* of the French; and in Brazil, where even palms of the genus *Desmoncus* furnish examples of these, they are called by the Brazilian Portuguese *Sipós*. The name "bush-ropes" is generally applied to them in the English colonies.

Bignoniaceæ.—This order embraces in it many large trees, as well as climbing and twining plants. In these twiners we find a peculiar organisation. The woody tissue is separated into a number of rays—varying in number—the wanting portion in which is filled up by cellular tissue derived from the bark (fig. 81), owing to the wood, after the liana is some years old, not forming on the four points of the cross passing through the pith (*éc*), and these being afterwards filled up by the increase of the bark at such places. There may be more than four points thus filled up by bark, owing to a similar process going on in the four subdivisions of woody rays, these again being further subdivided, until a stem may show four, eight, sixteen, or even thirty-two such rays separated by infringements of the bark. In *Tecoma radicans* the woody mass may increase, not by the exterior, as is the universal case among Dicotyledons, but even by the interior, at its limits where it surrounds the pith (Sanio).

Malpighiaceæ.—In this order, which possesses many twiners, the stem is traversed longitudinally by deep furrows, which sometimes even penetrate to the heart of the stem, dividing it into a number of pieces, each of which is covered by bark, and in some cases possesses a portion of the medullary canal also. In other cases, only one of the pieces into which the furrows separate it contains the medullary canal. All these pieces are united together by prolongations of cellular tissue, and in a few cases a general external bark surrounds the whole; so that the divisions would not be suspected from looking at the outside of the stem.

Fig. 80.—Piece of a liana of the order Malpighiaceæ, which looks like a strongly-twisted cable composed of several strands. We see also in the section that the woody strands are separated for the most part one from another.

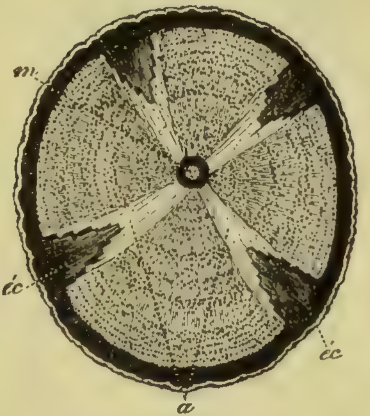


Fig. 81.—Transverse section of the stem of a liana of the order *Bignoniaceæ*. *m* Pith; *éc éc* Bark buried in the woody mass; *a* Bands of wood, sensibly modified, which extend between the pith or the bark forced into its angles.

In fig. 80 is shown a rope-like liana of this order, in which the general character of a liana, as well as the particular structure of the stems of this order, are seen. We see here also the curious fact, that as these lianas increase in age, the bark penetrates so deeply into the wood as often to separate the semi-isolated pieces; and when the stem is dry they separate altogether, as in the figure.

Menispermaceæ.—In the twiners of this order (especially in the genera *Cocculus* and *Cissampelos*) the woody layers develop only at one or two points on one side of the stem, while on the other there is no increase whatever. According to Decaisne,[1] the stem of the Menispermaceæ shows: (1.) fibres of the liber elongated, and with thick walls around the internal woody zone; (2.) between the posterior woody layers a parenchyma, resulting from the division of the fibres of the liber with their walls; (3.) the woody layers, of which a few only are circular, the greater number being unilateral (fig. 82).

Fig. 82.—Transverse section of a stem of a liana of the order Menispermaceæ.

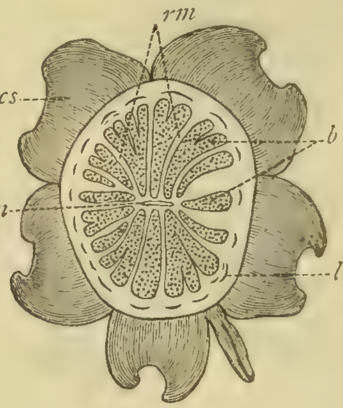


Fig. 83.—Transverse section of an aged stem of *Aristolochia cymbifera*, Mart.

Aristolochiaceæ.—In this order, of which the greater portion are twiners, Decaisne describes the stem as having the following organisation: Exteriorly, the suberous layer of the bark is considerably developed (fig. 83, *cs*), but without forming a continuous coherent zone, but rather disposed in irregular, almost distinct projections. Interiorly, the wood (*b*) is arranged about the pith (*m*), not cylindrically, but divided by the large medullary rays (*rm*) into ligneous wedges, and more or less divided externally again in a fan-shaped form by secondary rays. Opposite the woody bundles or their

---

[1] Archives du Muséum, vol. i., 1839 (Mém. sur les Lardizabalées). See also Radlkofer in Flora, 1858, S. 193.

subdivisions are little bundles of liber (*lb*), each of which appears on transverse section like a small bow.

Bauhinia.—In some members of this genus of twiners (order *Leguminosæ*) the woody fibres are not disposed in concentric circles. They form kinds of vertical and irregular bands, separated by cellular tissue, with the medullary canal excentric.[1] The stem itself, as in fig. 84, is curiously twisted in and out in a "crimped" manner. Duchartre, from whom we copy the figure, thus describes this peculiarity: During the first year the woody zones are two—a very small number—circular and concentric; but some of them are not produced in more than two narrow portions on opposite sides of the circumference of the stem. Accordingly, we may describe each of the crimped stems as presenting to the right or to the left of a regular centre and central pith two large opposite woody wings. In order to complete this irregularity, the ribbon-like stem bulges out greatly at each production of leaves, which are attached, after the alternate arrangement, on the sides of two surfaces of the stem. The result is a series of bulgings, according to the disposition of the leaf, by which the stem assumes a sort of crimped appearance. The bark covers all the exterior of this irregular woody ribbon. There are even more complex arrangements

Fig. 84.—Portion of the stem of a *Bauhinia*, the base (*a*) of which is almost rounded and caniliculated, whilst the portion higher up becomes crimped, alternately to the right and left; *a'* Section of the crimped portion; *f f f* Points of the attachments of leaves.

---

[1] Lindley, Introd. to Botany, p. 78, fig. 35 (*vide* Richard).

among the species of Bauhinia, but the above will suffice to exemplify the more common anomalies.

We may, however, touch briefly upon a few others much less common and less known — such as Phytocrene, described by Griffith in Wallich's Plantæ Asiaticæ rariores, iii. t. 216, in which, according to the figure given by Lindley, the "wood consists of plates containing vessels and woody tissue having no connection with each other, and separated at very considerable intervals by a large mass of prosenchymatous cellular tissue, filled with dotted ducts (bothrenchyma), and representing medullary rays. When the stem is dry, the woody plates separate from the other tissue, in which they finally lie loose."

In *Stauntonia latifolia*, *Euonymus tingens*, and in a *Pisonia* from Burmah, Lindley has minutely[1] described various peculiar anomalies in the stem. Dr Hooker has described and figured[2] an interesting anomaly in *Myzodendron brachystachyum*, one of the Zoranthaceæ, while M. Duchartre has described another anomaly in the stem of *Lathræa clandestina*, a herbaceous plant, the peculiarity being the absence of a medullary sheath and medullary rays. In *Melampyrum sylvaticum*, belonging to an order (Scrophulariaceæ) nearly allied to that (Orobanchaceæ) to which Lathræa belongs, an identical structure is found.[3] However, Brongniart described in the Crassulaceæ—a very different order—a somewhat similar structure (see also p. 84).

Endogenous Stems.—There is not a great number of anomalous stems belonging to this division. *Yucca*, however, in one species at least, arranges its woody bundles in concentric circles; while *Smilax*, an endogenous stem, but an exogenous *root*, approaches in structure the *stem* of Exogens. In grasses the stem is hollow, except at the nodes.

TERATOLOGY OF THE STEM.[4]

We have seen that in some cases the plant may be very short-stemmed, or, as it is called, *acaulescent;* but a monstrosity occasionally occurs, in which a stemmed plant becomes almost entirely stemless, or only presents the stem in the form of short, hard, woody tubercles, thickly clothed with deformed leaves covered with hairs longer and denser than usual. Again, the branches may be arrested in their development. This is of very common

---

[1] Introd. to Botany, i. 213, 218.

[2] Flora Antarctica, i. 298.

[3] Ann. Nat. Hist., vol. xv.

[4] Masters, Vegetable Teratology, p. 53, 455.

occurrence in the birch, when the branch ceases to grow in length; at the same time thickening into a bulbous knob at the end, from which are developed numerous small twigs, whose direction is sometimes exactly the reverse of that of the main branch. The branches of the spruce fir, under the attack of a species of insect (an aphis), are apt to be developed into cone-like excrescences. Spines, we have seen, are only abortive branches; and sometimes under cultivation the spines develop into true branches.

Trunks sometimes unite together, as in the case of the plane-trees of Buyukdere, near Constantinople, in which nine trees are wholly or partially united together. A similar deformity is sometimes seen in roots. In *Abies pectinata* and *A. excelsa* we will have occasion to notice the natural grafting of roots together —a very common occurrence. Bulbs cut in two may be united, and throw up a united stem; and if the two bulbs are of different coloured flowered varieties, the flowers on either side will be of different colours, or sometimes even with the two colours blended together.[1]

Though, as a rule, only closely allied plants can be grafted together, yet authenticated cases are on record in which widely different plants adhered naturally—*e.g.*, the union of the "haulms" of wheat and rye, of a species of *Sophora* to an elder (*Sambucus*). In like manner it has been found possible to ingraft the carrot and the beet, and the white and red varieties of the beet, together, though in none of these cases are the plants thoroughly joined, the adhesion being little more than the simple contact of living tissues; while, in the words of Dr Masters, "new matter is formed all round the cut surfaces, so that the latter become gradually embedded in the newly-formed matter." "Knaurs," again, are knots which form on the stem on some trees, particularly species of hawthorn, in the form of woody masses, from the size of a pea to a cocoa-nut, and which seem shortened branches. They may even be used for the purpose of propagation. The stem may be sometimes, as a monstrosity, enlarged; it may be divided; or, finally, as in the case of bulbs, be sometimes multiplied in number.

DIFFERENT FORMS AND TECHNICAL DESCRIPTIVE TERMS APPLIED TO THE STEM.

The technical terms used to designate the form, consistence, direction, state of the surface, &c., of stems, are numerous; and to have given them in the body of this chapter would be merely to reconvert Botany, as it was in former times, into a mass of names, and a botanical text-book into a vocabulary of the science. I have

---

[1] Darwin, Plants and An. under Domestication, i. 395.

accordingly followed M. Duchartre in this, as in other chapters, in his admirable method of classifying all these in a tabular form, so that at a glance the student may see the term he is in search of. These tables are not to be learned at once, but to be continually referred to during the progress of the student's studies. If he has access to a museum or garden, then he should continually endeavour to see specimens of each plant, whereon the character given can be studied. Without eventually mastering the technical terms of botany by constant reference to the plants, the science of description will become tedious and unsatisfactory; while, if the contrary method is adopted, it will be insensibly mastered, with comparatively little trouble, and the knowledge will be permanent.

1. **Direction.**—An upright stem (caulis erectus), raised vertically, as it is in most cases. *Ex.* Yellow loosestrife (*Lysimachia vulgaris*), Mentha sylvestris. *Rectus*, straight, and *strictus*, expressing a more absolute degree of straightness, are also terms used by the older systematists; while *laxus* or *diffusus* (loosely spreading) has a contrary meaning, as in *Sedum acre* (stonecrop), &c.

Ascending (ascendens), rising vertically after its lower portion has been lying horizontally; in other words, ascending obliquely. Ex. *Panicum sanguinale* (fingered Panicum), *Veronica spicata*, *Trifolium pratense*, &c.

Nutant (cernuus, nutans), with the summit bent. Ex. *Polygonatum multiflorum* (Solomon's seal).

Flexuose or *zigzag* (flexuosus), forming angles alternately from right to left and from left to right. Ex. *Statice reticulata* (matted sea-lavender), &c.

Tufted or *cespitose* (cæspitosa), "when very short, close, and many together form the same stock" (Bentham). Ex. *Carex cæspitosa.*

Decumbent (decumbens), bending down and leaning on the earth on account of its feebleness. *Ex.* Wood loosestrife (*Lysimachia nemorum.*)

Prostrate or *depressed* (procumbens, prostratus, depressus, humifusus), trailing on the ground. Ex. *Coldenia procumbens*, *Polygonum aviculare*, *Coronopus Ruellii* (Swine's-cress), &c.

Creeping (repens, reptans), spread upon the ground, sending out roots at short distances along its length. *Ex.* Creeping crowfoot (*Ranunculus repens*), and creeping loosestrife (*Lysimachia nummularia*), *Potentilla reptans*, &c.

Climbing (scandens), when it attaches itself to other upright stems or other bodies in order to support itself, either by spiral tendrils, as in the vine (*Vitis*), various species of passion-flower (*Passiflora*), and bryony (*Bryonia dioica*), or by adventitious rootlets, as in ivy (*Hedera helix*), when it is sometimes called *radicans*.

Voluble (volubilis), twining itself round other bodies by its own spiral form. *Ex.* Black bryony (*Tamus communis*), honeysuckles (*Lonicera*), French bean (*Phaseolus vulgaris*), &c. (See p. 78.)

2. Ramification.

Simple (simplex), not dividing. Ex. *Verbascum thapsus* (great mullein).

Ramose (ramosus), dividing into branches more or less numerous. *Ex.* Nearly all trees.

N.B.—The terms *alternè ramosus* (alternately branched), as in *Polygonum minus*, *Dianthus deltoides* (maiden pink), &c.; *determinatè ramosus* (abruptly branched), "when each branch, after terminating in flowers, produces a number of fresh shoots in a circular form from just below the origin of the flowers" (*e.g.*, *Erica tetralix*, and many other heaths, &c.); *Ramosissimus* (much branched); *distichus* (two ranked), when the branches spread in two horizontal directions, as in silver fir; *brachiatus* (bracheate, or four ranked), "when they spread in four directions, crossing each other alternately in pairs," a very common mode of growth in shrubs that have opposite leaves, as the common lilac (*Syringa vulgaris*), &c.,—are refinements of definition still used occasionally and commonly by the older authors, such as Sir J. E. Smith and the immediate followers of Linnæus.

Deliquescent (decompositus, deliquescens), branched from the base, so that it has few divisions. *Ex.* Most deciduous trees. The opposite of this is *excurrent*, as in most fir-trees, where the main trunk runs the whole length of the tree, giving off branches in its course.

Dichotomous (dichotomus). Ex. *Valerianella olitoria* (corn-salad).	When each point where it divides forms a bifurcation in the first instance, a trifurcation in the second, &c.
Trichotomous (trichotomus). Ex. *Nyctago hortensis*, &c.	

Stoloniferous (stolonifer, reptans), emitting stolons (p. 106). Ex. *Chlora perfoliata*, *Cerastium vulgare*, &c.

Flagelliferous (flagellifer), emitting towards the base slender leafless branches called *flagellæ*, which (as in the strawberry) root and form a new plant. *Flagellæ* and *stolons* are often confounded under the same name. Ex. *Saxifraga flagelliforme* of the Arctic Regions.

3. Consistence.

Herbaceous (herbaceus), soft and generally green.

Woody (lignosus), lignified, and more or less hard in the interior.

Fleshy or *succulent* (carnosus, succulentus), formed for the greater part of cellular tissue, more or less gorged with sap. *Ex.* Cactaceæ.

Medullose (Medullosus), with a large pith or medulla. *Ex.* Elder or bone tree (*Sambucus*).

Fistulose (fistulosus), with a central cavity (p. 83), which forms a tube in each internode. The contrary expression is *solid* (solidus). Ex. *Inula crithmoides* (golden samphire), most of the order Umbelliferæ, &c.

4. Form.—*Cylindrical* or *terate* (teres), showing, on transverse section, a circular form. Ex. *Trollius Europæus* (globe-flower), *Hydrangea hortensis* (hydrangea), &c. Half-terate (semiteres) is another term occasionally used.

Compressed (compressus), more or less flattened laterally.

This compression leads to the stem getting more or less determinate forms, expressed by such terms as—

Two-edged (anceps), compressed and forming two opposite angles. Ex. *Sisyrinchium striatum*, and most of the genus *Lathyrus*.

Angular (angulosus, angulare), with angles, the prefix being determined by the number present, *e.g.*—

Triangulare (triangularis). Ex. *Cactus triangularis*, *Carex acuta*, *Scorpis sylvaticus*.

Quadrangulare (quadrangulus). Ex. *Lamium album*, and other labiatæ.

Quinquangulare (pentagonal). Ex. *Asparagus horridus*, &c.

With three, four, five angles, and so on. Some descriptive botanists reserve these terms for stems in which the angles are acute, and talk about trigonal, tetragonal, pentagonal stems, and so on, when there are three, four, five, or other obtuse angles.

Sulcate (sulcatus), furrowed with longitudinal grooves. Ex. *Smyrnium Olusatrum* (common Alexanders), *Conium maculatum* (hemlock). When the furrows are finer the stem is *striated* (striatus). Ex. *Œnanthe fistulosa* (water dropwort).

Nodose (nodosus), having the nodes more visibly swollen out.

Articulate (articulatus), when the nodes easily separate. *Ex.* Samphire, *Stellaria*, *Geranium*, Indian figs (various species of Cactaceæ), &c.

Globular or *meloniform* (globosus, meloniformis), ball-shaped. Ex. *Echinocactus*, fig. 51.

5. Form and Elasticity.

Rigid (rigidus, strictus). Ex. *Sonchus oleraceus* (Sow-thistle), by opposition *flexible* (flexibilis).

Slender (gracilis), long in comparison with its thickness. Ex. *Orchis maculata* (spotted orchid), *Stellaria holostea* (chickweed), &c.

Sarmentose (sarmentosus), woody, long, and slender. *Ex.* Vine, honeysuckle, clematis.

Weak (debilis), *slender* (gracilis), and the opposite *swollen* (crassus).

Filiform (filiformis). Ex. *Zanichellia palustris* (horned pondweed), *Hydrocotyle vulgaris* (marsh pennywort). *Setaceous* (setaceus). *Capillary* (capillaris). Ex. *Eleoharis acicularis.*	All comparative forms of the same term.

Virgate (virgatus), "rod-shaped," woody, straight, stiff, and somewhat slender.

6. Structure and Covering.

Foliose (foliosus), and the opposite, *leafless* or *aphyllous* (aphyllus).

Winged (alatus), the leafy blades rather prolonged into two wing-like prolongations. Ex. *Passiflora alata*, *Lathyrus latifolius*, and other Leguminosæ, *Carduus acanthoides*, &c.

Suberose (suberosus), covered by a layer of cork. Ex. *Quercus suber*, *Ulmus suberosa.*

Rimose (rimosus), the bark swollen, cracked, and wrinkled. Ex. *Ulmus campestris*, *Castanea vesca.*

Spinose (spinosus), armed with spines. Ex. *Gleditschia*, &c.

Warty (verrucosus), with small callous excrescences. Ex. *Euonymus verrucosus.*

Aculeate (aculeatus), armed with prickles. Ex. *Rosa spinossima*, *Echinopanax horridum*, &c.

Unarmed (inermis), without anything of that sort.

Smooth (lævis), with smooth surface. Ex. *Euonymus Europæus.*

Rough (asper, scaber). Ex. *Equisetum hyemale, Jasione montana* (sheep's-bit), &c.

The expressions by which the presence or absence of hairs, asperities, &c., are designated on stems or other organs, being employed chiefly for leaves, will be explained at the end of that chapter.[1]

SUMMARY.

The stem is not usually present in the lower orders of plants, but, though much abbreviated, is almost invariably in some form a part of the structure of the members of the higher classes of the vegetable kingdom. In size, consistence, &c., it varies much, and gives rise to the various forms of plants popularly known, according to their size, as trees, shrubs, &c. There are three great classes of stems, divided, according to their structure, into Exogenous, Endogenous, and Acrogenous—these three classes corresponding with the three classes of plants known as Dicotyledonous, Monocotyledonous, and Acotyledonous. The first class has a pith, medullary sheath, concentric layers of wood, cambium, and a bark consisting of Liber or Endophlœum, Mesophlœum, Epiphlœum, and Epidermis; the second has no concentric layers of wood, but woody bundles scattered through a cellular mass—the bark being in union with the wood—though each of these woody bundles (as in palms) is composed of elements corresponding to the structure of the Exogenous stem; the third grows by the summit, and shows on transverse section vascular bundles, which grow simultaneously and are connected with the leaves, surrounding a central cellular mass. The development of each of these stems is different. There are also among the Exogenous stems various anomalous forms, which can, however, be referred to the type without much difficulty. There are also subterranean or terrestrial growing stems usually classed as roots, such as the rhizome (iris), sobol (couch-grass), tuber (potato), corm (crocus), stolon (rooting branch), sucker (asparagus), runner (strawberry), bulb (hyacinth), &c. A spine is an abortive branch, and a tendril is often a thread-like leafless branch, though it sometimes belongs to leaves when its character is different. Stems are

---

[1] These are all—and more than all—the technical terms the student will be likely to meet with in descriptions of the stem; but there are many more, mostly obsolete,—the older descriptive botanists perfectly luxuriating in a barren wealth of terms applied to the stem and leaf; and their writings bristle with these bits of barbarous Latinity, to define most of which would require a medieval metaphysician!

variously shaped, branched, &c., and numerous technical terms are used to express these modifications.[1]

[1] **Bibl.**, Mohl (on the liber) in Bot. Zeit. xiii. (1855), 873, or in Ann. des Sc. Nat., 4e sér., v. 141 (1856); Mirbel, Mémoir sur le Liber, and papers in Ann. des Sc. Nat., 2e sér., xx.; Naudin in ibid., 3e sér., i.; Trecul in ibid., 3e sér., xvii.; Henfrey in Ann. of Nat. Hist., 2e sér., i.; Schacht, Lehrbuch der Anat. und Phys. Gewæchse, and Der Baum, 216, 301-334; Clos, Cladodes et axes ailés in Mém. de l'Acad. des Sciences de Toulouse, 1861; Chatin in Comptes rendus, lx. 611 (27th March 1865); Hanstein Untersuch. über der Bau u. d. Entwick. d. Baumrinde (1853); Radlkofer in Flora, 1858 (§§ 193-206), and Ann. des Sc. Nat., x. (1858); Naegli, Beiträge zur Wiss. Botanik (1858), Heft I.; das Dickenwachsthum des Stengels . . . bei den Sapindaceen (1864); Gaudichaud, Recherches sur l'organographie, &c. (1841); Rauwenhoff, Archives Néerlandaises, v. 1870; and various papers by Van Tieghen, Tulasne, Caspary, &c., in addition to the authorities quoted in the text.

CHAPTER II.

THE ROOT.

The Root (radix) or descending axis of the plant is that portion of the vegetable organism which fixes it in the soil, extracts the nourishment from the medium in which the plant grows, and performs other minor functions necessary to vegetable life. In early life the stem and the root are in reality one; but in the more mature state of the plant, though continuous one with the other, and in some respects insensibly graduating into one another, yet a tolerably certain line can be drawn between them. The root has no perfect bark, and only a thin epidermis, and few or no stomata; it has no true pith, and no medullary sheath; it has no true leaves, but only cellular papillæ and absorbing hairs. It has in general, however, no true leaf-buds either, though an exception is found in Mountain peony, *Pyrus Japonica*, *Anemone Japonica*, &c. Finally, the root, unlike the stem, grows not throughout its entire length, but chiefly at the end. The roots of some plants, like the plum, apple, poplar, and hawthorn, may produce buds when cut off from the parent plant during the growing season, and are therefore capable of being propagated by root-cuttings. In the vast majority of cases the root is fixed in the earth, from which it absorbs the nourishment necessary for the growth of the plant; but in the case of the parasitic plants known as *epiphytes*, such as the mistletoe (*Viscum*), broomrape (*Orobanche*), &c., the plant derives its nourishment from some other plant on which it fixes itself. In the case of water-plants, like the duck-weed (*Lemna*), the water is the medium in which the root exercises its functions; and in the orders *Orchidaceæ*, *Bromeliaceæ*, *Aroideæ*, &c., many species derive their nourishment from the moisture contained in the air alone, the plants twining themselves on trees, with the roots suspended in mid-air. Accordingly, roots may be divided, according to their function, and the medium in which they exercise this function, into — 1. *Terrestrial;* 2. *Aerial;* and 3. *Aquatic.*

In most of the lower cryptogamic plants, such as lichens and Algæ, there is no true root, the roots so called being merely *fulcra* to attach the plant to the rock or other substance on which it grows, and in no way performing the absorbing function of a true root, these plants being cellular throughout, and absorbing their nutriment over their entire superficies. In the case also of the ivy (*Hedera helix*), similar fulcra or *crampons* arise from the stem and fix it to the wall or tree on which it grows, though it has been doubted whether these crampons of the ivy do not in reality absorb nourishment, the ivy often growing after its connection with the soil has been severed (fig. 85).

Fig. 85.—Fragment of the stem of ivy, showing the crampons *r r*, by which it attaches itself; *t* The stem.

In *Ampelopsis* similar thread-like tendrils, terminated by a disc-like sucker, come out from the stem and fasten the plant to the wall or other support on which it climbs. These tendrils, like those of the vine, are only modified branches. In *A. Veitchii* they originate from the development of a large branching hair from every cell of the epidermis of the part of the club-shaped end of the tendril, which is next to the body to be adhered to. They have little tendency to coil round any fixed object; and, like the branches of the plant on which they are found, turn away from the light, thus affording a good example of what has been called "negative heliotropism." In the cells of the tendril, crystals of oxalate of lime are found.[1] In *A. hederacea*, Darwin found that one tendril with five discs supported a weight of 10 lb.

In the dodder (*Cuscuta*) the roots take the form of suckers (*haustoria*), arranged along the stem, which attach the plant as a parasite to some other (fig. 86). These are, however, of the nature of true roots, absorbing sap from the plant the dodder is parasitic on, eventually destroying it; while in the case of the ivy, the death of the plant round which it winds itself is effected by a species of strangling or compression of the sap-vessels. In the dodder there is at first a true root absorbing nourishment from the soil; but it dies away as soon as the suckers are properly developed, leaving the plant dependent for nourishment on them alone: while in the case of the ivy the fulcra remain throughout life. The root is the first part of the plant which comes out of the seed, and varies in the rapidity of its growth in comparison with the stem in different species. In some it grows rapidly, and the stem slowly; in others quite the reverse. Again, some plants—

---

[1] W. R. M'Nab, Trans. Bot. Soc. Edin., xi. 293.

as many Coniferæ—are remarkable for the great development of the stem compared with the comparatively feeble development of root; while in others—such as the common *Medicago lupulina* or "nonsuch"—the length of the root is out of all proportion to the length of the stem. In *Megarhiza*, a genus of North-West American Cucurbitaceæ (gourd order), the plants of which are comparatively small in size, the root is as large as a flour-cask. The looseness or compactness of the soil has an effect on the shortness or length of the roots; and in sandy downs the root penetrates deeper and deeper in order to find the moisture it requires. In a rich and tenacious soil the roots of the maize will reach but 2 or 3 feet; while in a sandy soil they have been traced 15 feet. Lucerne roots occasionally acquire a length of 30 feet. The roots of the *Capparis spinosa* will often be 40 feet in length, and those of the ash as much as 95 feet. Moisture also has the effect of increasing the length and the ramification of roots, as can be well seen when these enter drains and often choke them up entirely.

Fig. 86. — Dodder (*Cuscuta major*) in flower, attached to a fragment of a living stem. At *a* we see five suckers ranged in a row, by which the plant extracts its nourishment from the plant to which it clings.

It was found by Sachs[1] that the roots of a plant accustomed to grow in earth were not unable to exercise their functions in water, and the roots of water-plants in earth, but that new roots were in either case developed to suit the new medium in which the plant found itself—these new roots, however, being anatomically the same as their predecessors. When parsnips, carrots, and liquorice-roots are grown in sand, they become covered with delicate bristle-like filaments. The *Phleum nodosum* of some authors is only a variety of *P. pratense* (timothy grass) grown in a dry soil; in damp soil it is fibrous and luxuriant. *Alopecurus geniculatus* (marsh fox-tail grass), which has naturally a fibrous, creeping root, has been known to develop an ovate juicy bulb when grown on the top of a dry wall. Though the action of light is unfavourable to the growth of roots, yet it is not absolutely fatal; for a root will develop itself to its full dimensions without ever touching the soil,

---

[1] Botanische Zeitung, 1860, p. 113.

as when plants are germinated on a wet sponge, and then transferred to water, as in the numerous experiments of Sachs and

Fig. 87.—*Cephælis Ipecacuanha*, showing the long annulated root used in medicine.

others. In these experiments, maize and other plants germinated, grew, leafed, flowered, and fruited, without ever touching a particle of soil. However, if a plant thus germinated on a wet sponge, or similar medium, be transferred to the soil, it will die if not frequently watered; but if a plant grown in water, but *started in the soil*, is similarly treated, it will be quite unaffected, and grow without any more water than what may be contained in an ordinary soil. Plants of dry countries—like the Pampas of America—are very intolerant of moisture; and if care is not taken to keep their roots from moisture, except in very slight amount, they will droop.

DEVELOPMENT.

When the seed of a dicotyledonous plant is subjected to germinating influences (moisture, heat, and the oxygen of the air), a swelling begins to appear, which results in the embryo bursting its enveloping coats, and the radicle appearing. This radicle—the commencement of the future root—immediately, if the position of the seed permits it, or if not, as soon as possible by a circuitous route, if necessary—directs itself downward into the earth. It is always the inferior or radicular extremity of the embryo which develops itself into the radicle, continuous with the stem, which is to continue it upwards—a circumstance Richard considered characteristic of the Dicotyledons, and which he styled by the name *Exorhizal* (ἔξω, out of; *ριζα*, root). This radicle, as soon as it has fairly got fixed in the soil, begins to throw out on every side more minute threads—radiculæ or rootlets—which fibres in their turn rapidly branch, until the original axis (or caudex) is soon surrounded by them, the petiole forming a subterranean tree-like mass, which, as a

Fig. 88.—Simple tap-root of *Anacyclus Pyrethrum.*

Fig. 89.—Branched tap-root of a *Ratantica.*

whole, we call *the root.* In some cases these radiculæ are never sufficient in number to surpass the original root in importance, that part always maintaining its original pre-eminence ; but in other cases, the radicles increase so in number and size that the original structure is entirely concealed by the fibres which it had given birth to. In the first case, the root is called a *tap-root* (fig. 88) ;[1] in the *second,* a fibrous root (fig. 89). The amount of roots on a plant is very much more than is usually supposed, it being difficult to extricate them entire from the earth. Schubart found the roots of winter wheat penetrated as deep as seven feet in a light subsoil forty-seven days after sowing, and that the quantity of roots in proportion to the entire plant decreases from forty per cent on the last day of April to twenty-four per cent in May. Hellriegel estimated the length of the roots of a barley plant in a vigorous condition at 132 feet, and that of an oat plant at 154 feet ; and that only $\frac{1}{10}$th of a cubic foot of soil would suffice for a barley plant, and $\frac{1}{32}$d of a cubic foot for an oat plant to develop in it. Tap-rooted plants seek their nourishment generally at a greater depth than fibrous-rooted ones, which spread through the subsoil, and are accordingly more affected by wet and drought than the former.

Development of the Roots of Monocotyledons.—The development of the root in this class of plants (grasses, &c.) is different from that of dicotyledons. In the great majority of cases, the radicle, as it pierces the lower part of the embryo, is covered with a cellular sheath, and gives rise to numerous fibrillæ, which are similarly covered. This covering Mirbel terms the *Coleorhiza ;*[2] and Richard, to distinguish their mode of development from that of dicotyledons, called them Endorhizal.[3] In after-life they generally retain this compound character, though, if the plant is perennial, the first-formed roots die, to give place to others formed farther from the central axis of the plant.[4]

Schleiden and other authors are inclined to think that there is no true root in monocotyledons, but that what goes under that name is merely an adventitious root, such as is developed when a cutting of a plant is placed in the soil. A great number of monocotyledons have, however, no coleorhiza on their roots. The true radicle remains a rudimentary axis, as Planchon shows in *Aponogeton distachyum*, for a short time, or, as in the palms, for a much longer period ; but more ordinarily it is of shorter duration,

---

[1] *Racine pivotante* of the French botanists.

[2] Κολεός, sheath ; ῥίζα, a root.

[3] 'Ενδον, within.

[4] We must, however, remember that this Endorhizal and Exorhizal character of the roots in Mono- and Di- cotyledons, is not universal, and that there are various exceptions to the rule. Palms, *e. g.*, have exorhizal roots, while the Indian Cress (Tropæolum, a Dicotyledon) has endorhizal ones.

and is replaced by the adventitious roots, which are transitorily developed round the base, or are entirely confined to the inferior portion of the stem, or they may appear gradually higher and higher up. But in certain species the stem, getting gradually little by little lost, is finally supported, as in the case of the *Iriartea exorhiza*, an American palm, by these adventitious roots, at a height of three or four feet above the earth. In a word, although in monocotyledons the true radicle is developed at germination, yet it scarcely shows itself, and disappears more or less completely. In every case it is of secondary importance; and the nutrition of the plant depends upon the secondary or adventitious roots, which are produced either at first, or soon after the plant has commenced an independent life.

Elongation of the Root.—Duhamel, and more recently and exactly E. Ohlerts,[1] have shown that the root increases in length by its inferior extremity, and that the growth is limited to a space about one-sixth of an inch from the tip. Wiegand, who has made similar experiments, showed that the lengthening was chiefly manifested towards the outer extremity of the roots. Dividing the young radicle of a sprouted pea into four equal parts, by ink-marks, he found that after three days the first two divisions next the seed had scarcely lengthened at all, while the third was double, and the fourth eight times, its previous length. This arrangement permits the thin thread-like radicles of plants, which are the chief parts concerned in nutrition, to penetrate into every crevice among rocks, and to seek nourishment in the most impervious soils. If the main roots of a tree meet with an insurmountable obstacle to their elongation, they will concentrate all their energy on the radicles, which increase in great numbers. Hence gardeners, when they wish to transplant a bush or small tree without danger, cut off its tap-root, the result of which is that radicles are developed, when it can be more safely removed. The autumn, when the year's growth is completed, and the leaves become inactive, and the rootlets also cease their functions and get covered with a thickish epidermis, is the best time for transplanting.

Rhizotaxis.—We shall by-and-by see that the leaves are arranged on the branches according to certain fixed mathematical laws, and that even the branches themselves are not placed on the trunk without order. At first sight it might be supposed that the radicles were produced around the caudex without any approach to order, though, knowing that the root bears an analogous character to the rest of the tree above ground, we might expect to find somewhat similar laws regulating its structure. In the middle of the last century, Bonnet first announced that the radicles in the haricot, pea, bean, buckwheat (*Fagoprum esculenteum*, Mœnch.),

---

[1] Einige Bemerkungen über die Wurzelzasern.—Linnea, 1837, p. 609-631.

were arranged around the caudex in four exact parallel lines, at equal distances the one from the other; and subsequently a number of other botanists have announced various observations on the same subject regarding other plants. The most complete of these are, however, those of Clos,[1] who has made what he calls *Rhizotaxis* the subject of two elaborate memoirs. The regular arrangement of the radicles on the main axis is chiefly observed in the young plant, and gets less and less apparent as the plant increases in age. All the radicles on every root are produced one above another, so that they appear on the root in the form of longitudinal lines. However, in a certain number of cases the lines follow an oblique and not a rigorously vertical course. This Clos calls "the law of superposition." The number of these longitudinal rows is fixed and determined either for the plants of the same order, or for those of the same genus, or at least for the individuals of the same species. The rows are separated from each other by equal spaces; and in number, according to the vigour of the plant, are from two to five, the latter number being rare. The radicles are arranged in two lines in the orders *Papaveraceæ*, *Cruciferæ*, *Resedaceæ*, and *Geraniaceæ;* in four lines in *Malvaceæ*, *Euphorbiaceæ*, *Umbelliferæ*, *Labiatæ*, *Verbenaceæ*, &c. The number three is much rarer than the preceding, and is observed in some *Leguminosæ—e. g.*, in the genera *Vicia*, *Trifolium*, *Lathyrus*, *Coronilla*, &c. The number five is even less frequent, and is seen in the *Compositæ*, where, however, the number two is not rare; and again in the *Solanaceæ*. This remarkable arrangement is, according to M. Clos, connected with the disposition and number of fibro-vascular bundles in the root of the plant.[2]

STRUCTURE OF THE ROOT.

Pileorhiza.—This structure, so named by Trecul[3] (πῖλος, cap; ῥίζα, root), consists of a thin layer of loose cells surrounding the growing point of the root like a sheath. In *Lemna* it is well developed, and sometimes called in that plant the ampulla. It effectually protects the tender floating root from the shock of foreign bodies, and against the attack of minute animals. Coniferæ have the pileorhiza well developed, though in chestnuts, birches, and other trees it is thinner. On the adventitious roots of one of the screw-pines (*Pandanus odoratissimus*) it is remarkably well developed. When the root of this tree dries and contracts, the pileorhiza is

---

[1] Ebauche de la Rhizotaxie, 1848; and Ann. des Sc. Nat., 1852, t. xviii.

[2] Duchartre, l. c. 208.

[3] Duchartre thinks that, according to strict etymology, it should be *pilorhiza*. The German *wurzelhaube* and *wurzelmütze* mean the same thing.

seen covering it like a long hat. It is also well developed in *Coniferæ*. According to Schacht,[1] the pileorhiza is occupied by some longitudinal rows of cells, which sometimes contain starch and surmount the growing point of the root. The rest of this cap consists of layers of cells parallel to the external surface. It is produced at the growing extremity of the root by the disintegration or casting off of the cells which form that portion, and which, after disengaging themselves from the cell-tissues proper, soon die, merely forming an elastic cap to protect the tender point of the root. In 1849, Goldman[2] showed that after the germination of the plant the radicle detached a yellowish mucilage in which are very delicate cells, feebly united together, constituting probably the commencement of the pileorhiza and the early cell-exfoliation which in after-life keeps it up. The cells of the pileorhiza are filled with air instead of sap.

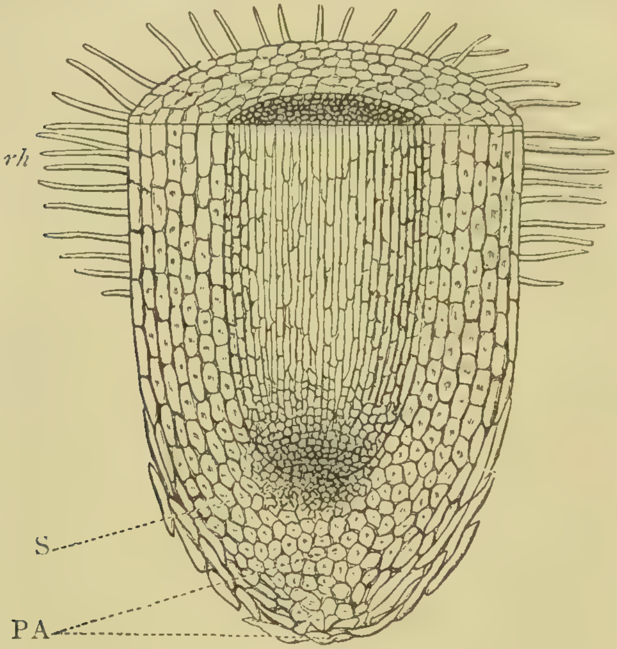


Fig. 90.—Extremity of the root cut longitudinally, much magnified. It shows the radicle hairs (*rh*), the pileorhiza PA, and the growing and absorbing point S. The so-called "spongioles" are shown as loose cells near the extremity.

Spongioles.—The growing point of the root is covered by the pileorhiza, and is attached to the middle of that cap. It is composed, like every growing point, of very delicate minute cells in the midst of growing parenchyma, and only differs from the cellular mass, which forms the growing point of the stem, in that the latter gives birth to leaves and the rest of the axis, and the

---

[1] Flora, 1853, No. 17.

[2] Bot. Zeitung, 1849, p. 884.

former gives rise only to the continuation of the root. This point is called the *spongiole* or spongiolet, from a mistaken idea of its absorbent function. It was at one time commonly taught that this was the growing and absorbing point of the root. This is not so. The growing point of the root is just behind the apex, and there the root increases by multiplication of cells, casting off the old ones, which constitute these so-called spongiolets which terminate every final subdivision of the root. Ohlerts[1] and Link[2] showed that not only are they not the absorbents of the root, but in reality that they are denser than the rest of the tissue, and in all likelihood perform that function, if at all, only to the most limited extent (fig. 90).

General Structure of the Root. *Dicotyledons.*—The general structure of the root is very similar to that of the stem, but with various differences. The *pith* is not always found in the root (*e. g.*, *Cicuta virosa*), and when found is in general reduced to a mere thread,[3] and with no medullary sheath. In the radicles it is difficult to recognise it. The *wood* of the root is produced in annual zones, as in the stem, but the analogous elements composing it are in the root much larger than in the stem—the fibres, cells, and vessels of the woody parenchyma being in the former to the extent of twice, or even four times, the same elements in the stem. For instance, in the wood-cells of the roots of Coniferæ there are, instead of a single file of areolar discs, two to four longitudinal rows of these. On the other hand, the *medullary* rays in the root are much less numerous and distinctly marked than in the stem; and the fibres in the root are irregularly interlaced, so that on that account the roots are rarely of use in carpentry. The *bark* in the root has all the anatomical elements arrayed in the same order as in the stem. It differs, however, in the larger size of the fibres of the *liber*, in the greater development which the cellular envelope often attains in the root, particularly of herbaceous plants, and in the stem possessing a much greater development of the suberous layers of the bark. There is no *chlorophyll*, except in aerial roots. The *cambium* is rich in nitrogenous substances, and the cells of the root often contain crystals.

The slight development of cork is in consequence of the root-tissues being so short a time in a growing condition, so that, before the suberous layer has time to form, the vitality has departed from these tissues. The *Epidermis*[4] is very thin, and not always present in a perfect form. Its cuticle has rarely stomata, but it is often covered in its young state with hairs, which are generally simple, but in some plants, such as *Saxifraga sarmentosa*,

---

[1] Linnea, 1837, s. 609.

[2] Ann. des Sc. Nat., ser. 3, xiv. 10.

[3] Schacht, Lehrbuch der Botanik, &c., ii. s. 173.

[4] Sometimes called the *Epiblema*, a most unnecessary multiplication of terms.

Anemone apennina, *Opuntia ficus indica*, *Calendula micrantha*, and *Brassica Rapa*, are branched. These *radicle hairs* serve the purpose of absorbents. They have been studied with great care by Gasparrini. They are very minute, and consist of tubular elongations of the external layer of root-cells; and through them the actual root-surface exposed to the soil becomes something incalculable. The older roots lose their hairs, and suffer a thickening of the outermost layer of cells; these dense-walled and nearly impervious cells cohere together and form a rind which is not found in the young and active roots (Johnson). These hairs are most abundant in plants growing in poor soils, and on roots with dense surfaces, such as the *Cactaceæ*, *Euphorbiaceæ*, pines, the *Hydrocharis*, &c. The silver fir (*Abies picea*), and other species of that genus, have no root-hairs; but this want is compensated by the delicate absorbing cuticle and the great number of rootlets, which, perishing before they become superficially indurated, are continually replaced by new ones during the growing season.[1] They are also wanting in *Monotropa hypopitys* (yellow bird's-nest), and *Cicuta virosa* (water-hemlock). The root-hairs adhere very closely to the soil, and are very active in their function of absorption over the newly-formed part of the roots, where alone they are found.

Monocotyledons.—In monocotyledons there is a considerable difference between the structure of the root and the stem. (1.) In palms there is a large cortical zone, swollen, loose, and spongy, and a great central woody mass not divided into distinct scattered bundles as in the stem, and surrounding a mass of parenchyma, remarkable for its series of vessels decreasing in size from within outwards, and the presence of unrollable tracheæ. (2.) In *other monocotyledons* the root is very similar to that of the palms in possessing the continuous fibro-vascular zone; but, on the other hand, is remarkable in possessing one or more layers of thick-walled hard cells, which Schleiden has compared to a kind of sheath (*Kernscheide*). It is well seen in plants of the genus *Smilax*. (3.) Certain epiphytal Orchids and Arads have, as we have already noticed, aerial roots, which have been the subject of considerable research among botanists, who are by no means agreed as to their nature. They are in colour grey or white, often bright-coloured, and their extremities more or less green. Schleiden's description of the structure of these aerial roots in *Pothos crassinervis* may be taken as the type of all. The roots in this plant are provided with a peculiar epidermis possessing stomata, which corresponds to the pileorhiza in subterranean roots. The semi-lunar cells of the stomata are filled with a brown granular matter, and are elevated above the surface of the epidermis, and form a special tissue

---

[1] Schacht, Der Baum, p. 165.

whose walls exhibit the most delicate spiral fibres.[1] These spiral cells are full of air, a fact which explains the white colour of the roots containing them. The cells at the extremity of the root are full of liquid, which allows the green parenchyma lying under them to be seen. This layer of fibrous cells Schleiden called the *Valamen radicum* or root-veil (Wurzelhülle), Chatin the *epidermoidal membrane*, and Oudeman the *Endoderm*—each of these botanists differing in opinion regarding its character, which is as yet imperfectly known.

Acotyledons.—In vascular cryptogams the structure of the root shows a simple central vascular bundle, immediately surrounded by a cellular bark, which in its turn is covered by an epidermis composed of two layers of cells, and which bears a number of hairs, these hairs differing from the radicle hairs already described in the higher classes of plants by their brown colour and large size. The centre of the vascular bundle presents no sign of pith. In ferns and Equisetaceæ the root and stem are strikingly different. In Lycopodiaceæ, however, the stem is simply the central vascular bundles ; but in this order of plants the root is again distinguished from the stem, in so far that in the former the cellular zone which surrounded the vascular bundles is formed of cells much smaller and closer than those in the stem. In these plants the root springs from any part of the spore, and hence to the roots of this great division has been given the name of *Heterorhizal.*[2]

ADVENTITIOUS ROOTS.

These occur normally in many plants, and may be produced from cuttings, even from leaves when placed in favourable situations ; but they usually spring from plants in moist, warm, shady places, as in the depth of the tropical forests. Palms and other such trees are particularly distinguished by the possession of them. In Madeira and Teneriffe, *Laurus Canariensis*, a large tree, sends out during the autumn a great number of adventitious or air roots, which surround the stem and grow to the thickness of the finger ; in the following autumn they dry and fall to the ground, giving place to new ones. Indian corn, oat, buckwheat, valerian (fig. 91), grape vine, and other plants of temperate regions, if subjected to the combined influence of heat, moisture, and shade, will often produce these air-roots. Contrary to the opinion of Unger and Chatin, Duchartre,[3] as already mentioned,

---

[1] Principles, p. 79. Link (Elem. Phil. Bot., p. 393) first discovered this layer.

[2] Ἕτερος, diverse.

[3] Expériences sur la végétation des plantes épiphytes, Journ. de la Soc. impér. et centr. d'Hort., ii. 67, 79.

thinks that these air-roots do not absorb moisture from the air, but dew and rain; the first-named view is probably more correct. In these aerial roots there are scale-like leaves, and the epidermis is green, but, unlike the underground root, they produce no fibrillæ or rootlets. In Epiphytes, De Luca detected all the inorganic constituents of plants. Their absorbing power is probably also assisted by the spongy envelope of their roots collecting water to yield it up to their other root-tissues.[1]

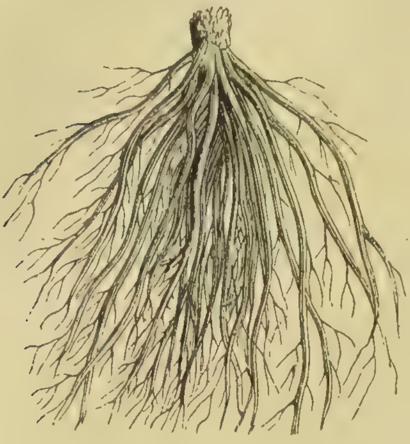


Fig. 91.—Fasciculated adventitious roots of *Valeriana officinale.*

In the case of the screw-pine, *Pandanus*, and other palms, &c., these adventitious roots attain great dimensions, coming out from the stem at a height of several feet from the base of the trunk. In the gigantic banyan tree (*Ficus Indica*), which flourishes on the banks of the river Nerbuddah in India (and which tradition reports to have sheltered Alexander the Great), the adventitious roots are so large as to appear like trunks springing (as they also do in the mangrove) from both trunk and branches; so that this tree is composed of 350 large trunks and more than 3000 smaller ones. At one time, before part of it was carried away by floods, it was capable, it is said, of sheltering 10,000 men; but even yet, 7000 people could repose under its shade.

These adventitious roots often proceed from places where the epidermis has been injured (as frequently is the case in the olive), or where the sap has met with some obstacle to its free circulation, and, in particular, at those knots or nodosities which occur accidentally on the stem and branches. In the screw-pine they follow a spiral order of development. Often (as in the mangrove) the main root will decay, and the plant be entirely dependent on these aerial roots. In this last-named tree—so characteristic of the low, swampy, sickly shores of various countries—the tendency to sprout in the air is shown even in the embryo, which begins to germinate while the fruit is yet attached to the parent branch, often elongating its radicle to the length of a foot or more before the fruit falls to the ground.

The *Lianas*, or woody climbers, which obstruct the tropical forests of the Isthmus of Panama and Nicaragua, send out these aerial roots freely; many of which reach the ground, when they enlarge in diameter and form new trunk-like supports. When cut

---

[1] Chatin, Comptes rendus, 1856.

in two, the lower end of the severed stem sends down a root to re-establish its connection with the ground. Lévy, a French traveller in Nicaragua, finding one belonging to a species of *Bignonia* in this condition, from which hung roots a foot long, cut them off; two days afterwards it had produced new roots of the same length. Cutting it again, it promptly gave out new roots, but more slender ones. He repeated the process up to the eighth time, but the new roots were now so slender and feeble that he desisted.[1]

In some plants (the vine, for instance) adventitious roots are produced as the result of circumstances impairing the proper action of the ordinary subterranean roots; and in old willows, in which the stem is more or less decayed below, adventitious roots will be produced on the upper part of the tree, as seemingly an attempt to obtain fresh supplies through a more vigorous and healthy channel.[2]

Deciduous roots.—According to Munter, the roots of the yellow water-lily (*Nuphar lutea*) are deciduous, leaving on the rhizome holes about the size of peas, and very like in appearance to the human acetabulum, and at the bottom of the pit a bundle of broken-off woody fibre, not unlike the *ligamentum teres*, marking the places where the roots separated spontaneously. Even while the root is attached to the rhizome, the bark of the latter is raised to give origin to the protuberance (or "limbus" as he calls it) which surrounds the edge of each little hole.[3]

FUNCTIONS OF ROOTS.

A knowledge of the physiology of the root is of the highest importance in understanding the growth of the plant, for on it depends the nutrition of the vegetable organism. Its chief functions may be considered under the heads of fixation, absorption, and respiration, as a magazine of nutriment, and as a dubious organ of excretion.

(1.) **As an Organ of Fixation.**—Without being fixed in the soil, the plant would be unable to extract the nutriment by which its tissues are formed. This is a necessity of plant-life so manifest that it is unnecessary to do further than mention a proposition so self-evident. It has, however, been supposed that the cruciferous plant popularly known as the "rose" of Jericho (*Anastatica hierochuntica*, L.) was an exception to the rule that all plants must be fixed; but in reality it is not, for it only gets unrooted when it dies

---

[1] Bull. Bot. Soc. Fr., Nov. 1869.

[2] Masters, Teratology, 156; see also Trecul, Ann. Sc. Nat., v. 340, and vi. 303.

[3] Annals of Nat. Hist., xvi. 236.

away: and the other example of the "manna" which often falls in the desert is equally fatal to the idea mentioned, for the plant is a lichen (*Sphærothallia esculentea*, Nees.), which, though often carried up in great quantities by the wind, is naturally attached to tiny fragments of rock. The *Lemna*, which seems to float in the water, is equally a proof that a plant must be rooted; for the medium from which the plant extracts its nourishment must be looked upon in the light of its soil.

The position of the root, buried in the soil, enables it to escape the trying vicissitudes of climate to which the rest of the plant above the soil is subjected—the heat of summer and the winter's cold—and so assists in preserving the life of the plant. Equally it has an effect in modifying the coldness of the sap when the ground is of a low temperature, and in cooling it when the soil is arid and burning, though in reality this effect has been much exaggerated by theorists,—the sap in summer never having a noxious degree of warmth; and in winter, when the sap is very cold, there is little or no circulation of juices.

(2.) **Absorption.**—All nutriment must pass into the plant in either a liquid or gaseous state. Solid particles, no matter how minute or how delicately suspended in liquid, cannot enter the circulatory system of the plant. Every part of the root—with perhaps the exception of the "spongioles"—which is young and delicate, is constantly performing this office, and only ceases to do so when the parts get impervious by the formation of the suberous layer in the bark, or by the thickening of the epidermal cells. When the radicle hairs are present, they perform an important part in the function of absorption. Hence Gasparrini called them *Suckers*. As soon as the parts of the epidermis on which they are situated cease to absorb, these radicle hairs die away, but are renewed on the newer and pervious surfaces of the rootlets. It has also been found by the experiments of De Saussure that each plant can take up from the soil a different amount of each substance contained in it, even though these substances should be all in the same proportion in the soil originally; in other words, roots have a selective power, and only take up what is necessary for their life, and in the proper proportions too. Saussure considered that this preference of a plant for one substance before another in the same liquid was due to the different degrees of fluidity or viscosity of the different substances; so that the rootlets of the plant are filters of the most perfect and delicate description possible. This simple mechanical explanation is not, however, held by all botanists—some maintaining that the faculty of selection by roots is allied to an instinct. But this doctrine is difficult to hold in the teeth of the well-known fact that they will absorb the most energetic poisons, which will produce on their organism fatal effects; but probably the poisons so deaden and destroy the delicate tissues as to render their power of selection inert. On this theory—that roots are capable of selecting the materials useful for the plant to which they belong, and of rejecting materials unnecessary or innocuous—is founded the whole doctrine of the "rotation of crops," so universally adopted by modern agriculturists. The force with which active roots absorb moisture is very great. Hales found that in the spring time the pressure exerted on a gauge attached to the stump of a grape vine supported a column of mercury 32½ inches high, or equal to a column of water 36½ feet high. Subsequently, Hofmeister found that in a potted kidney-bean (*Phaseolus multiflorus*) the force of the ascending sap could support 6 inches of mercury, in the nettle 14, and in the vine 29 inches. Heat increases, and cold decreases or altogether stops, the absorbing power of the roots. Roots can perform their functions under extraordinary circumstances. Sonnerat discovered in the island of Lucon a rivulet the water of which was so hot that a thermometer immersed in it rose to 174° Fahr. Swallows, when flying over it, dropped down motionless. Notwithstanding this heat, he observed on the banks two species of Aspalathus and a species of vine (*Vitex Agnus-Castus*), which with their roots swept the water. In the island of Tanno, the Fosters, who accompanied Captain Cook round the world, found the ground near a volcano as hot as 210° Fahr., and at the same time covered with flowers.[1]

(3.) **Respiration.**—Roots, though buried in the earth, require air just as much as do the leaves, and equally die if they cannot come under its influence. To this is probably partly due the fact of roots seeking and often filling up drains. The experiments of De Saussure showed that if roots are plunged into hydrogen, nitrogen, and, above all, carbonic acid gas, the plant will die in the course of a few days. This fact explains why often in cities trees die when their roots are subjected to the influence of soil impregnated with ordinary coal-gas escaping from the neighbouring pipes, or from entering sewers where various noxious gases are emanating. It also shows the advantage of frequently loosening the soil around plants so that air as well as moisture may the more easily reach their roots. For the same reason trees should not be surrounded by pavement if they are to be kept in good health. Hence stones in soil are really beneficial—in so far that by preventing the finely powdered earth being caked by rain, they allow of a freer access of air to the roots. One of the earliest observers who called attention to the practical application of the above fact was our friend Mr Anderson—Henry, who observed that some cuttings placed in water which was not aerated, and over which a film sufficient to exclude the air had gathered, threw

---

[1] Willdenow's Principles of Bot. (English Trans., 1811), p. 262.

out roots from the stems above, but not from those parts which were beneath the water.

(4.) **The Root as a Magazine of Nutriment.**—In fleshy roots like the turnip and carrot the absorption is chiefly through the small radicles or rootlets which go off from the main root or caudex—this portion serving the purpose of a storehouse for sugar, pectose, and other nutritive matters, which in these *biennial* plants are required to support the plant during the exhaustive flowering season in the second year. After the carrot or other such plant has flowered, it is found that the caudex is quite exhausted of its nutrient matter. The farmer, by increasing by means of cultivation the size of his root crops, increases the store of nourishing matter, and then, by removing them from the soil in the autumn, he preserves for the use of his stock the nutrient substances which would otherwise have gone in the ensuing summer to support the growth of flowers and seed.[1] In terrestrial orchids (fig. 89) there is a store of starch and gum contained in the tubercular swellings of the roots which is applied to the nutrition of the plant. In other roots, such as those of *Spondias tuberosa* (hog-plum), the tubercles contain a large quantity of clear fluid—in the example mentioned, upwards of a pint; and in certain plants found in the Desert of Sahara this store of water, according to Livingstone, serves an important use among the inhabitants of that arid waste.

Fig. 92.—Tubercles of *Orchis maculata.* These tubercles give the character to the "scrotiform" or "palmate" root of the older authors. By some French writers they are called "Ophrydo-bulbs."

(5.) **As a Floating Organ.**—A fifth use of roots may be noted. Charles Martins[2] has shown that in certain aquatic species of the genus *Jussiæa,* some of the roots are transformed into ovoid or cylindrical swimming bladders, composed of a lacunary tissue filled with air (p. 32), in order to sustain the plant in the water. In most aquatic plants this *rôle* is performed by

---

[1] Johnson, How Crops Grow, p. 241.

[2] Mém. de l'Académie de Montpellier, vi. 352; and Bull. Soc. Botanique de France, xiii. 169.

transformed leaves, as in *Utricularia vulgaris*, *Trapa natans*, *Aldrovandra vesiculosa*, &c.

(6.) **Excretion of Roots; Antipathies and Sympathies of Plants.**—Some agriculturists believe that they have observed facts sufficiently numerous to show that certain plants are noxious to those which grow alongside of them. Thus, they say that darnel-grass (*Lolium temulentum*), flea-bane (*Erigeron acris*), are hurtful to wheat; the creeping thistle (*Cirsium arvense*) to oats; purple spurge (*Euphorbia Peplus*) and field scabious (*Knautia arvensis*) to flax; corn-spurry (*Spergula arvensis*) to buckwheat (*Fagopyrum esculenteum*),—and so on, with a long list of other plants in cultivation. In a word, they consider that certain plants show antipathies to others; and this is due to the fact that the roots of these plants excrete matters which are injurious or even fatal to the life of the plants which are supposed to be antipathetic to them. On the other hand, it is believed that some plants are sympathetic towards others. Thus, wheat is popularly supposed to be an excellent crop to precede any leguminous plant, and that this is due to the fact that the wheat has excreted some substance or substances from its roots which is beneficial to the life of the peas or beans. This is a very old doctrine, espoused as early as the days of Duhamel, and since then discussed by Brugmans, Plenck, Humboldt, Macaire-Prinseps, De Candolle, Bouchardat, Chatin, Bracconet, Cauvet, Unger, Meyen, Walser, Trinchinetti, Garreau, Brawers, Sachs, and other distinguished observers, and rests solely on the idea that roots have the power of excretion. Have they, then, this power? It appears, from numerous observations by the most accurate observers, that there is really no such function in roots, and that any facts which might be supposed to fortify a contrary view rest on insufficient grounds, and are referable to other causes. Accordingly, the idea of antipathetic and sympathetic plants is not proved. Indeed, even supposing that these excretions could remain in the soil long without undergoing chemical change, it is difficult to see how many plants could grow on the same field if this were true; or how, if a plant sends out noxious substances into the soil, great tracts of country could be covered with the same species; how forests could be composed of different species; or, indeed, how an isolated tree could flourish for hundreds of years in a soil impregnated with its own excretions. Each plant has, however, the power of making the soil less suited for others of the same species, or of other species of the same family which succeed it, though improving it for species of another family. Oaks, for example, render the soil more suitable for firs, and *vice versa*.—See "Nutrition," chap. v.

DIFFERENT FORMS OF ROOTS.

There are numerous modifications of roots, owing to the varied situations in which it is necessary for them to pursue their functions. These different forms may, however, be referred to their *duration*, their *situation*, their *division*, their *consistence*, their *form*, and the character of their surface—an arrangement M. Duchartre has adopted, with the result of considerably simplifying the subject, and in which, with some alterations and additions, I have followed him in this and other chapters.[1] It is not, however, always possible to accurately define the different forms—one running into the other by various intermediate gradations.

1. Duration.

Annual (radix annua), duration limited to one year—*i.e.*, such plants die after one flowering season.

Biennial (biennis), living two years; in other words, they flower in the year succeeding that in which they are sown. Annuals and biennials are sometimes included under the term *Monocarpic*,[2] which De Candolle applied to them.

Perennial (perennis), living more than two years.[3] To these the term *Caulocarpic* is in like manner sometimes applied, in contradistinction to rhizocarpic, used in reference to herbaceous plants. In a *herbaceous perennial* the only part which remains after flowering is a small perennial portion in or close to the earth, called the *stock*. The other kinds of perennials are shrubs, trees, &c.

2. Situation.

Subterranean (subterranea), the ordinary case.

Aquatic (aquatica), floating in water. Ex. *Lemna*, *Utricularia*, *Trapa natans*, &c.

Aerial (aeria), the major part out of the earth—orchids, &c. In older books the term was often applied to roots growing on some part exposed to the air—*e.g.*, such parasitic plants as mistletoe.

---

[1] Similar tables will be found in that remarkable book, Gray's Natural Arrangement of British Plants, vol. i. (1828).

[2] Μονος, alone, and καρπός, fruit; while Perennials were called *Polycarpic*—πολὺς, many, and καρπὸς, fruit.

[3] The duration of the root determines that of the plant, except in the case of those plants which replace the original root by adventitious ones. Many plants which are perennial or even woody in warm countries, when transported to temperate or northern countries, become annual—*e. g.*, *Cobæa scandens*, *Nyctago hortensis* (shrubs in Chili and Peru), *Ricinus communis*, the castor-oil plant, which is in Africa and America a considerable tree, &c.—See section ii. chap. i., "Flowering."

3. Direction.

Relative to the earth.	*Perpendicular* (perpendicularis), descending vertically. *Ex.* Daucus (carrot), ash (Fraxinus), oak (Quercus).
	Oblique (obliqua), *horizontal* (horizontalis), words which explain themselves.
	Descending (descendens.)
Relative to the root considered in itself.	*Straight* (recta), going in a straight line.
	Curved (curvata), describing a curve.
	Flexuose (flexuosa), describing a sinuous curve.
	Contorted (contorta). *Ex.* Bistort, &c.

4. Division.

Entire at the base (stirpata), or the main axis of the root predominating.	*Simple* (simplex), undivided, or scarcely ramified, &c. *Ex.* Carrot, beet.
	Ramose (ramosa), more or less ramified. *Ex.* Most trees and shrubs. When there are (as in *Rhododendron*, *Erica*, &c.) numerous capillary ramifications, the root is sometimes called *Comose.*
Multiplied at the base (multiceps)—that is to say, with the main axis of the root either equally ramified or wanting.	*Fibrous* (fibrosa), composed of a number of smaller-sized roots or radicles. *Ex.* Many grasses—*i.e.*, *Poa annua*, *Anthoxanthum odoratum*, and most annual plants. When the radicles are thinner, the term *capillary* (capillaris) is sometimes applied.
	Funiform (funiformis), union of roots resembling cords. *Ex.* Palms, Pandanus, &c.
	Fasciculated or *tuberiform* (fasciculata, tuberiformis), like a fibrous root, but with the fibres swollen into the form of spindles. Ex. *Ranunculus Ficaria*, *Asphodelus luteus*, &c.
	Grumose (grumosa), union of numerous parts, short, interlaced, and fleshy—smaller in volume.

5. Form.

Tap (palaris), with a single descending mass, well marked (fig. 88, p. 128). *Ex.* All Dicotyledons in earliest stage. In advanced state the dock (*Rumex*) is a good example. The tap-root is the *Racine pivotante* of the French.

Conical (conica), in the form of an inverted cone, rather thin. *Ex.* Carrot.

Fusiform (fusiformis), spindle-shaped. *Ex.* Parsnip, radish, and many biennial plants.

Napiform (napiformis), in the form of a top, short and swollen. *Ex.* Turnip.

Rotund (rotunda), more or less round.

Nodose or *Coralline* (nodosa), showing a necklace-like form, having numerous swellings with short interspaces. Ex. *Corallorhiza innata.*

Moniliform (incrassata), swollen either at the base, in the middle, or towards its extremity. Ex. *Pelargonium triste.* In the last case it is sometimes called *filipendulous*, from its resemblance to the root of *Spiræa filipendula*, L. (dropwort).

Tuberose (tuberosa), swollen either in one or in many masses, generally ovoid, or irregularly in masses called tubercles (tubera). The greater part, however, of these tubercles are formed, not by the root, but by the stem or its modifications (*vide* Stem). Ex. *Vicia lathyroides*, *Trifolium glomeratum*, many *Orchidaceæ*, &c.

Premorse (præmorsa), when the axis ends abruptly, as if bitten off. Ex. *Scabiosa succisa* (devil's bit), *Leontodon autumnalis* (autumnal hawbit), *Hedypnois hirta*, and various species of *Hieracium.*

6. Surface.

Smooth (lævis).

Rugose (rugosa), marked by irregularities more or less defined.

Annulated (annulata), marked with superficial rings (fig. 87).

Carinated or *Keeled* (carinata), marked with a longitudinal keel-like protuberance, as in *Polygala Senega;* or there may be two or more such keels.

7. Consistence.

Woody (lignosa), all trees and under-shrubs;
Soft (tenera), *fleshy* (carnosa);
Hollow (cava), and its opposite;
Solid (solida),—are all words which explain themselves.

SUMMARY.

The root is the first part which leaves the embryo, and, according to the medium in which it exercises its function, may be terrestrial, aerial, and aquatic. The crampons of ivy fix it to an object; and the suckers of dodder, in addition to extracting nourishment from the plant (on which it is parasitic), fix it on the plant, and perform all the functions of roots after the parasite severs its connection with the soil. The length and development of roots depend a good deal on the soil. The roots of Monocotyledons are *endorhizal*, those of Dicotyledons *exorhizal*, while those of Acotyledons are *heterorhizal*—words referring to their method of springing from the embryo or the spore. The true roots of monocotyledons are soon replaced by adventitious roots, such as are seen in palms. The aerial roots absorb moisture from the air, and are possessed of several peculiar tissues. The radiculæ are arranged on the caudex in a regular mathematical order. The growing end of the root is the spongiole, which is covered by the cap-like Pileorhiza. In general structure the root has representatives of nearly all the tissues in the stem, and is much the same in structure, except in the case of monocotyledons, in which it somewhat differs from the stem. The root fixes the plant in the soil, and absorbs nutriment by all the tender young surfaces and by the radicle hairs. Roots also require air, and if deprived of it languish and die. The root is also in some plants a store of nutriment and water for the use of the plant. There is little ground for believing that roots excrete at all. The modifications of roots are various, and may be studied under the heads of Duration, Situation, Direction, Division, Form, Surface, and Consistence.[1]

---

[1] For further information in regard to the root, the following may be consulted: Trecul, Recherches sur l'origine des racines (Ann. des Sc. Nat., 1846, t. v. vi., and Bull. Soc. Bot. de Fr., 1855, ii. 106; Link in Ann. Sc. Nat., 1850, t. xiv.; Brauwers, ibid., 1858, x. 181-192; Gasparrini, Ricerche sulla natura dei succiatori (Naples, 1856); Bouchardat, Recherches sur la végétation (Paris, 1846); Trinchinetti, Sulla facoltà assorbente delli radici, (1843); Unger in Denkschrift. d. k. Akad. d. Wissensc., 1850, p. 75-82; Saussure, Recherches Chemiques, chap. iii.; Macaire in Mém. de la Soc. de Phys. et d'hist. nat. de Genève, v. 282-302; Cauvet, Etudes sur le rôle des racines dans l'absorption et l'excrétion (Strasbourg, 1861); Braconnot, Influence des plantes sur le sol (Ann. de Phys. et Chim., t. lxxii., 1839); Meyen, Neues system d. Pflanzen-Phys., t. ii.; Walser, Untersuchungen über die Wurzel-Ausscheidung (Tubingen, 1838); Naegli and Leitgib in Naegli's Beitragen zur wiss. Bot., Heft iv., 1867; Hofmeister, Allgem. Morpholog. der Gewæchse, 1868, § 5; Johannes Hanstein, Bot. Abhandlungen, 1870, Heft i.; Dodel, Jahrbruch. wiss. Bot., vii. s. 149 *et seq.*; Reinke, Wachsthumgesch. der Phanerogamen wurzel, in Hanstein's Bot. Untersuch. Heft iii. (1871), Flora, 1873; Klein, Ibid., 1872; Sachs, Lehrbuch, 145-152 (1873),—in addition to those papers and books quoted in the chapter.

CHAPTER III.

THE LEAF.

THE last of the three great organs necessary for the nutrition of the plant is the **leaf**,[1] and to a consideration of this important appendix of the stem we propose dedicating this chapter. It is at once an appendix to, and a prolongation of, the stem, and, looked at in its general aspect, is seen to be a mass of cellular tissue or *parenchyma* expanded over a fibrous framework—the ribs and veins. The cellular tissue is derived from the green layer of the bark (p. 91), while the framework of ribs and veins is continuous with the stem proper.

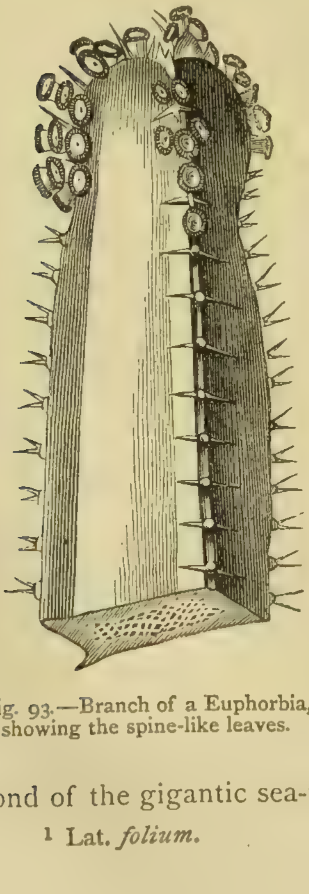


Fig. 93.—Branch of a Euphorbia, showing the spine-like leaves.

Some plants, like the dodder (Cuscata), have no leaves; while in others, such as some *Cactaceæ* (cactus or prickly pear order), they are reduced to the form of spines (figs. 51, 52, 93), the whole stem of the plant, though morphologically a stem, yet performing the functions of leaves. In another genus of the same order (*Pereskia*) there are regularly developed leaves; while on others, like *Opuntia*, there are caducous leaves in the young state of the plant, while the old ones are *aphyllous*,[2] or leafless, unless, indeed, the spines scattered over them be looked upon as leaves, or perhaps as persistent stipules. In some other plants the leaves are modified so as to become *phyllodia* (p. 151). Leaves are also of all shapes and of all sizes, from that of the great water-lily (*Victoria regia*) of the South American lakes and rivers, whereon water-birds stand while watching their prey, and the frond of the gigantic sea-weed of the South Pacific (*Macrocystis*),

---

[1] Lat. *folium*.

[2] A, privative; φύλλον, leaf.

which is often 800 feet in length, down to the minute representatives of this organ in the duckweed (*Lemna*) and the *Drabas*. The leaves of some palms of the genus *Rafia* are often 6 feet in length, and are used in Madagascar for aprons, or for roofing huts; while that of the Cabo palm is frequently employed as an umbrella or parasol. Palm-leaves were once very commonly, and in some countries are still, used for writing on. It is probable that the oldest books were many of them inscribed on this material. The single leaf of *Godwinia gigas*, Seem.—one of the Araceæ—measures more than 13 feet in length, the petiole alone measuring 10 feet.[1] With these generalities we may now enter upon a more minute study of the structure, development, arrangement, and functions of leaves. In doing so, we shall consider leaves under the following heads: 1. *General structure of the parts composing a simple leaf*; 2. *Microscopic Anatomy*; 3. *Development*; 4. *Præfoliation*; 5. *Venation*; 6. *Forms*; 7. *Phyllotaxis*; 8. *Uses*; 9. *Fall and Death*; 10. *Technical terms used in describing them.*

GENERAL STRUCTURE.

Take any *simple leaf*, such as that of the oak, laurel, elm, maple, &c. On examination, we shall find that it admits of being considered under the following aspects: 1. The *petiole*, or leaf-stalk; 2. The *lamina*, limb or blade; 3. The *midrib*, and its subdivisions, the *ribs*, &c.; 4. The *base*; 5. The *apex*; 6. The *margin*; 7. The *upper surface*; 8. The *under surface* (collectively called *Paginæ*). Under these heads let us briefly consider each of the parts named.

Petiole.—The petiole may be either present or wanting; the latter case is by no means an uncommon occurrence, and such leaves are said to be *sessile*. It also varies in length and shape. A very common condition is when it is *round*, or *semi-cylindrical*. In the aspen or trembling poplar (*Populus tremula*) it is *flattened* at right angles to the axis of the leaf, so that the slightest movement of the air affects the leaf in both directions; the result is the almost continual flutter of the leaf, which has given the tree its popular name in all languages, and interwoven with it many explanatory (*sic*) superstitions. In various plants (such as the butterbur[2] and artichoke) it is *channelled*. This structure is found in many alpine plants, though whether it subserves any peculiar function in the economy of these plants, as poetical botanists, such as Bernardin St Pierre, have supposed, is very dubious. In the corage tree, and in the sweet-pea, it is prolonged on either side in a

---

[1] Seemann and Trimen in Journ. of Bot., 1869, p. 313; Gardeners' Chronicle, 1869, p. 133, and 1873, p. 73 (M. T. Masters).

[2] *Petasites vulgaris*.

wing, and is said to be *alate;* in the latter plant this wing is *accurrent*—*i.e.*, it runs down the stem also in a continuation from the petiole. In grasses, sedges, &c., there is little or no distinction between the blade and the petiole, which in these plants is distinguished as a *ligule*, and instead of being articulated to the stem as in other plants, it embraces the stem more or less completely, when it is said to be *sheathing*, *vaginated*, or *amplexicaul*. In some of the Umbelliferæ, particularly of the genus *Angelica*, this sheath (*vagina*) is in the upper leaves developed at the expense of the other portions of the leaf, so as to form a large membranous envelope around the shoots and young flowers. The sheath in the Umbelliferæ is sometimes called the *pericladium*.[1] In a few species (such as *Strelitzia juncifolia*, a plant belonging to the Musaceæ or banana order) the limb is entirely undeveloped, and the petiole alone exists. It is generally continuous with the base of the leaf; but in *Hydrocotyle* (marsh pennywort), *Nelumbium* (sacred bean), &c., it is placed near the middle of the inferior surface of the leaf, and is said to be *peltate*. In a few plants with *opposite leaves* on the same level, the two expanded attachments of the petiole unite, so as to form what looks like a leaf composed of two equal portions, one on either side of the stem, which seems thus to go right through the middle of it. These leaves are said to be *connate*, and are exemplified in *Crassula perfossa*, Lamk., a common garden-plant, &c. It is, however, in all cases, necessarily continuous with the stem; and in many cases where it is *articulated*, the stem is swollen into a papilla (or *pulvinus*) of cellular tissue. In its minute structure the petiole is seen to be composed of four, five, or more bundles, which come out in an arcuate manner from the stem, and are composed of a woody portion composed of fibres, vessels (especially of the laticiferous type), and even medullary rays, and superiorly of spiral vessels derived from the medullary sheath. The whole is bound together by cellular tissue. These form its interior; while the cortical portion, forming a sheath to the vessels, is derived from the liber and cellular tissue, the whole being enveloped, like the rest of the stem and blade, by a common epidermis. The arrangements of these vessels, &c., are the same as in the stem; only, what in the stem is innermost is in the petiole uppermost, and what outermost is below. When the leaf falls, it leaves a scar (*cicatricula*) on the stem, on the surface of which can be seen a number of round dots of a uniform number and arrangement in each species. These dots indicate the number of woody bundles composing the petiole which have come out from the stem (fig. 50, *a*). The petiole in many plants is large and succulent. A familiar example is afforded by our ordinary garden rhubarb (various species of *Rheum*), the petioles of that plant

---

[1] Περί, around; κλάδος, a branch.

being the parts used as a culinary vegetable. The petiole and midribs of some species of palms are so large as to be used by the natives of the countries they are found in for making oars.

Lamina,[1] *midrib, veins*, and the general outline of the leaf, will be better considered at a future time. Suffice it to say, that on the blade and its different parts enumerated depend the shape and general character of the leaf,—the blade being the expanded and more or less flattened portion, which fulfils the various functions of the leaf; the petiole being only an accessory, and by no means absolutely indispensable portion of it. The margin may be either entire or divided in an almost endless manner, and may be either finely bevelled off, or level with, and of equal thickness with, the rest of the blade, which in its turn may be thick or thin, according to the anatomical structure and particular species in the economy of which it must play a part. Finally, the midrib and its subdivisions, which are continuations of the petiole, are as various in their distribution and character as any other portion of the leaf.

Accessory or modified parts of the Leaf.—Such, briefly, is the general structure of a typical leaf. There are, however, in many leaves certain modifications of these organs, or even accessory ones not hitherto described, to which separate names have been given, and which therefore require special notice. These are *Stipules* and *Phyllodia*.

Stipules. — These are little scale-like organs on each side of the petiole, either attached to it or separated from it, and are either persistent, or, as in the oak, beech, chestnut, and most other forest-trees, caducous. When attached, their union to the petiole may be more or less intimate: in some cases they are only united to the petiole by their base; while in the familiar instance of the rose, they are attached along their whole length, forming a wing on either side of the petiole. They are not, however, always lateral, but are sometimes *axillary* (fig. 94), and

Fig. 94.—Entire leaf of *Melianthus major*, L., with its axillary stipule *st*; *t* Fragment of the stem upon which the leaf is attached (about one-sixth nat. size).

---

[1] Also occasionally called the "merithal" (μὲρος, part ; θαλλὸς, blade).

membranous in structure, as seen in *Melianthus major* (great honey-flower), *Houttuynia cordata* (a Chinese plant), the genus *Polygonum*, and in the Polygonaceæ generally.

Stipules are not found in the vast majority of Monocotyledonous plants, and are also absent in all Dicotyledons with opposite leaves, and, with the exception of three or four orders, in Dicotyledons with alternate leaves where a sheath is apparent, &c. However, of late years Krause and Norman of Christiana have pointed out that certain Dicotyledons, particularly some *Cruciferæ*, which have been described as altogether wanting stipules, have these in an early condition of the plant, but that they are soon arrested in development, and remain either in a rudimentary condition or simulate the appearance of simple glands. Stipules frequently furnish useful character for the co-ordination of Natural orders—all the members of many orders either wanting or possessing such. For instance, they are found in the whole orders *Malvaceæ* (mallows), *Tiliaceæ* (limes), *Rosaceæ* (roses and brambles), *Leguminosæ* (beans and peas), *Urticaceæ* (nettle order), &c.; while, on the other hand, nearly all Monocotyledons, and among Dicotyledons *Labiatæ*, *Solanaceæ* (nightshade order), &c., are deprived of them.

Like leaves, stipules are various in form—*e.g.*, membranous or scale-like — and even, as in the locust-tree (*Robinia*), *Paliurus* (Christ's thorn), caper (*Capparis spinosa*), &c., are developed into spines. In melons, cucumbers, and most of the Cucurbitaceæ, their place is taken by tendrils. Sometimes they are only present on the developing shoots (*e.g.*, beech, fig, magnolia), when they form the covering of the buds, but fall off as the leaves expand, leaving behind them cicatrices of the same nature as those left by the leaf. Stipules generally show a strong inclination to cohere with each other, or with the base of the petiole. In some orders (such as the *Rubiaceæ*, hop, &c.) which have opposite leaves, the stipules are *interpetiolar*—*i. e.*, they occupy the place between the attachment of the petioles on each side. In the order just mentioned, and in some others, the stipules thus placed in contact unite

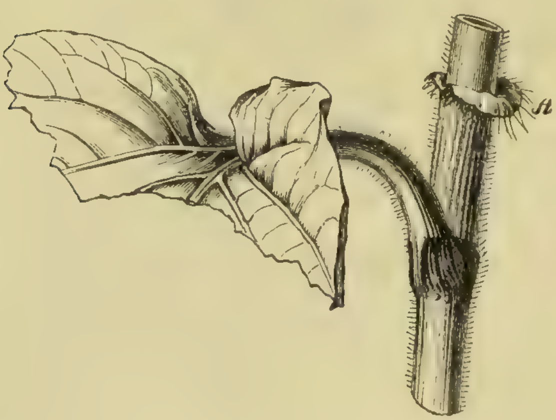


Fig. 95.—Base of the leaf of *Polygonum orientale*, L., the *ochrea st*, the truncated border of which spreads out, and is thickly ciliated.

to form what looks like a single pair of stipules for each pair of leaves.

Leaves possessing stipules are styled *stipular*, while the absence of them is denoted by the term *exstipular;* when adherent to two sides of the petiole they are *petiolar;* when free, or non-adherent, *caulinary* (mallow); when (as in the plane) both margins unite to form a sheath around the stem above the leaf, they are said to be *interfoliaceous;* and when, as in the Polygonaceæ, such a sheath is membranous, it is called an *ochrea* (fig. 95).[1] In a *compound leaf* (such as that of the bean), there is not only a common stipule at the base of the common petiole, but each leaflet has its own stipule—here designated, for the sake of distinction, a *stipel* or *stipella*, or little stipule. When a stipule (or indeed almost any part besides the leaves and flowers) is stalked, it is said to be *stipitate* (*stipes*, a stalk).

Though generally both stipules are exactly similar, yet those of *Ervum moncinthos* present an exception to this rule. In this plant one of the stipules is straight, linear, and acerose, while the other is enlarged and deeply divided.

What purpose the stipules serve in the economy of the plant is a question somewhat difficult to answer, especially when, as in some of the Coniferæ and other plants, they are rudimentary. Sometimes, as in the case of *Lathyrus aphaca* (yellow vetchling), they certainly supply the place of leaves—the true leaf in this plant being reduced to a spiral petiole with two large stipules. In other cases they are supplementary to leaves, and assist them in ministering to the nutrition of the plant. Though pronouncing on the final use of any organ is always a rash, and frequently a dangerous, exercise of the reasoning faculties, more especially since we know that many organs really serve no purpose in the economy, but are only landmarks left behind to show the course of the march of development, yet we may point out that in some cases the stipules serve to protect the young and delicate parts in the form of a kind of envelope. This is seen in many figs, particularly *Ficus elastica*, Roxb., *Magnolia*, in the submerged *Potamogetons*, &c.; when a great axillary embracing stipule entirely conceals the young leaf—and when the leaf increases and expands, it falls off in the form of a conical cap. In some cases the stipule forms the scaly envelope of some buds also.

Phyllodia.—In some plants the petiole takes the character of an expanded blade-like organ, traversed by veins mostly of the parallel character, and which is called a *phyllodium*.[2] It can, however, be distinguished from the lamina by being entire, and having the ribs parallel; while in the true leaf (the blade which in such a case usually disappears, though it is invariabl

uch stipules ‘ synochreate

[2] Φύλλον, leaf; εἶδος, form.

present at germination), it has netted veins. It may also be distinguished by being uniformly vertical, presenting its margins instead of, as in a true leaf, its upper and under surface to the sky and earth. Phyllodia also sometimes bear a true compound lamina at the apex. They constitute the whole foliage of various Australian *Acacias* (order *Leguminosæ*), hence the peculiar physiognomy of some portion of the landscape of that continent. In *Acacia heterophylla*, the leaf passes gradually and by successive stages from an ordinary compound bipinnate leaf to that in which it is completely converted into a phyllodium. In *Eucalyptus*—another Australian genus, belonging to the order Myrtaceæ—we find that the leaves are directed, not horizontally, but vertically. They cannot, however, be considered as phyllodia—their structure, with the exception of their abnormal direction, showing them to be true leaves.

Something very similar to "phyllodiniation" is shown in a variety of the common arrowhead, found in the vicinity of Paris (*Sagittaria sagittifolia*, *β*. vallisnerifolia), and which the describers, MM. Cosson and Germain de St Pierre, consider to be due to the action of the water,—only the leaves found at the surface have the ordinary sagittate form; while those submerged at the bottom of the water have a long ribbon-shaped petiole, either straight or a little enlarged towards its superior extremity.[1] A similar variety of the leaves is often produced in *Scirpus lacustris* (marsh sedge), when growing in a rapid stream.

Though in most cases (*e.g.*, the Acacias mentioned, and some woody species of *Oxalis*, or sorrel) it is easy enough to distinguish by the character we have given the phyllodium from the lamina, yet M. Duchartre has very justly pointed out that in some cases it is by no means easy to say which is phyllodium and which the lamina. For instance, De Candolle has declared that there are true phyllodia in the leaves of Hyacinths, Aloes, and even in the great proportion of Monocotyledons—an idea, however, which is scarcely tenable. Still it shows how difficult it is always to draw the line.

MICROSCOPIC ANATOMY.

No matter how different the external appearance, size, or contour of the leaf, the general microscopic structure is the same throughout the vegetable kingdom. The lamina is bounded by two surfaces—the superior and inferior, covered by the epidermis; between these two layers of epidermis lies the parenchyma, stretched on and between the ribs,—the whole forming what De Candolle has called the *mesophyll*,[2] or middle leaf, which, it ap-

---

[1] Flore de Paris, p. 321.

[2] Μὲσος, middle; φύλλον, leaf; also sometimes styled the *Diploë* (διπλοῖς, a

pears, is therefore made up of the ramifications of the veins, and the cellular parenchyma or tissue. This parenchyma is of great importance, for in it is contained the chlorophyll, which gives the familiar green colour to the leaves, and in the cells composing it the elaboration of the sap goes on until it is fitted to be distributed throughout the tissues for the nutrition of the plant. Let us now consider this structure somewhat more minutely.

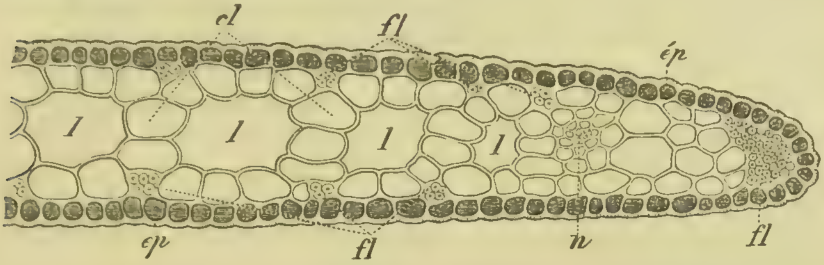


Fig. 96.—Transverse section of a leaf of *Zostera marina*, L., showing the aeriferous canals, *l l l l*, separated by partitions *cl*, formed by a single row of cells; *n* Nerves; *ép ép* Epidermis; *fl fl fl* Little bundles of very long straight cells, with very thick walls, believed by some to be liber-cells.

Normal Histology of a Leaf.

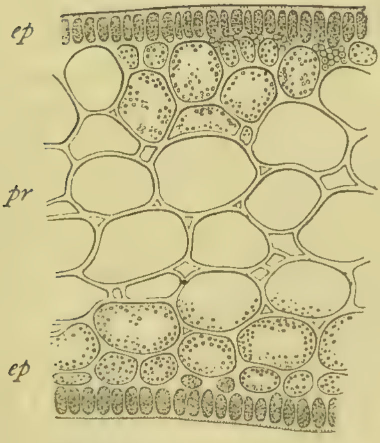


Fig. 97.—Transverse section of a leaf of *Posidonia Caulini*. *ep ep* Epidermis on both surfaces, with upright cells filled with chlorophyll; *pr* Parenchyma composed of large cells.

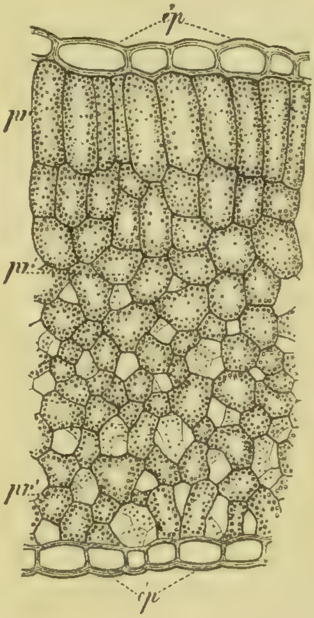


Fig. 98.—Transverse section of a leaf of *Pelargonium inquinans*, Ait., showing branched parenchyma, with lacunæ, *pr' pr'*, of which it is chiefly composed; *pr* "Palisaded" or upper layer of oblong or ovoid cells; *ép*, *ép*, Epidermis. The cells are filled with chlorophyll.

—Cut a thin *transverse* section (at right angles to the surface) of any of the more common leaves, such as that of the apple, pop-

---

covering). It has not, however, the most remote connection with the similarly named structure in the skull.

lar, beech, or cultivated "geranium" (fig. 98), and put it under the microscope. Then the following structure ought to be seen, commencing from the upper towards the under surface: First, there is a single layer of firm flattened epidermal cells; under these lie an upright row of more or less large rounded or elongated cells;[1] under these, again, is a loose parenchyma of smaller irregularly-shaped cells, loosely united together so as to leave numerous spaces between them; and finally, bounding the inferior surface, and forming its epidermis, is a similar flattened layer of epidermal cells, but *without* the vertical layer of elongated cells found immediately under the epidermis of the upper surface. The loose spaces between the cells of the middle parenchyma contain air, and communicate with each other; while here and there, in the midst of the cellular tissue, will be seen the cut ends of woody bundles —the ribs which ramify through it (fig. 96, *fl*). These *nerves*, as we have already seen, are a continuation of the petiole, and get smaller and smaller as they subdivide, until at last the most minute subdivisions consist simply of a spiral vessel with a few elongated cells.

The spongy *parenchyma*[2] is of a pale-green colour, and contains less chlorophyll than the upper row of vertical cells; and for this reason the under surface of the leaf is in general paler than the upper. The irregular network of cells, with open spaces, generally corresponding to the stomata, has also some effect on the paler character of the under surface of the leaf. The leaf chlorophyll also contains less iron than that of other portions of the plant. The under surface of leaves not being so exposed to the direct rays of the sun as the upper one may have also an effect in causing less development of chlorophyll on the under surface. Under the absence of light, it may be remarked, chlorophyll gets yellow, and loses its iron, and the juices, from being acrid and bitter, get mild and sweet; though, if the surface is exposed to light, the normal acridity and bitterness again return; the green colour and the iron likewise return at the same time. It is on this principle that celery is earthed up, in order that, by *blanching*, it may lose its natural acrid qualities.

The *epidermis* is composed of a flattened row of cells, the shape of which varies in different plants. They are, however, most regular in shape in monocotyledons, when they are arranged in lines, and of a parallelogramic shape (fig. 34). In many plants, especially in Dicotyledons, they are of a wavy irregular outline. The two forms may possibly be in some way connected with the different venation found in the leaves of these two great divisions of

---

[1] Sometimes called the *Palisaded* layer, from their resemblance to the palisades or pickets of a fence.

[2] Sometimes called Diachyma (δὶα, in midst; χῆμα, tissue).

plants (p. 73). In the stone-crop, house-leek, and suchlike plants, the epidermis is easily torn off; but in other cases the cells are so firmly coherent as to form a fine membrane. Like the same structure throughout the plant, the epidermis contains no chlorophyll, but is colourless, the green colour of leaves being owing to the chlorophyll contained in the parenchyma between, and which is seen through the transparent epidermal cells. While the parenchyma of leaves contains starch, chlorophyll, and even crystals of little soluble substances, the epidermal cells contain none of these. They are, however, richer in nitrogenous material. Essential oils and resins are secreted by special groups of cells, and contained in particular reservoirs, as is seen in the leaves of *Hypericum* (St John's wort), citron, orange, &c. These are spherical in the orange, cylindrical in conifers, &c.; but they are always surrounded by the cells which secrete the oil or resin. In *Urticaceæ*, *Acanthaceæ*, &c., are seen pediculated bodies (cystolithes) formed of cells, the walls of which are impregnated with carbonate of lime (p. 30). The leaves of many grasses, and the leaves of *Moquilea* and *Petræa*, are so impregnated with silex, that, if burnt, there will remain behind a perfect skeleton of the leaf, with the outline of the stomata and hairs.[1]

The object of this firm epidermis over the whole surface of the leaves, and especially on the upper surface, where it is assisted by the layer of vertical cells, is to prevent too rapid evaporation from the surface of the leaves. Accordingly, we find that in some plants which admit of copious evaporation there is more than one layer of epidermal and vertical cells. In the oleander, which we have already (p. 55) noted as remarkable for the stomata at the bottom of pits on the under surface of its leaves, the epidermis on the upper surface of the leaves is composed of three layers of thick-walled cells, and two layers of vertical cells. In most plants which thrive in a dry atmosphere the epidermis is thick; and it is owing to this very fact that they thrive. In plants such as the aloe, which bear great droughts, there is generally a thick epidermis. Furthermore, this layer of epidermal cells is waterproof from the deposition of wax, which either forms a coating inside the cells, and gives the glistening appearance to many *glaucous*-leaved plants, or appears in the form of a powdery "bloom," which easily rubs off, as familiarly seen in the cabbage, &c. In many plants which yield wax, it exists in a thick coat, as on some fruits.

In the *Cactaceæ*, the cells of the parenchyma beneath the epidermis are also much thickened by deposits, so as almost to obstruct exhalation through the epidermis; and it is probable, as Dr Gray remarks, that this may be found to be more common in leaves

---

[1] Schacht, Lehrbuch der Anat. u. Phys. d. Gewæchse, ii. s. 121.

which remain on the plant for more than one season, than we have hitherto supposed.

Exhalation is, however, absolutely necessary, in order that the plant may be enabled to concentrate the crude sap; and accordingly, a provision is made for this moderate and regulated evaporation in the stomata, the structure and character of which we have already discussed in our earlier studies of the microscopic structure of the plant (p. 54). With a very few exceptions (*Passerina hirsuta*, L., &c.), the under has always more hairs on its epidermis than the upper surface, though both, in most cases, support more or less of these cellular appendages, as well as glands of various kinds (p. 61).

Deviations from the Normal Structure.—Though the general structure of the vast number of leaves is as we have described it in the foregoing paragraphs, yet there are a few exceptional structures found. In an elementary treatise, space cannot be spared to note all of them, even were it advisable. A few, however, of the more remarkable may be called attention to. In many monocotyledons, and in some dicotyledons, there is no distinction between the loose lacunary parenchyma and the infra-epidermal vertical layer (the "palisaded cells"); and the whole parenchyma between the two layers of epidermis is composed of loose rounded cells, full of lacunæ (*e.g.*, in the hyacinth). Again, in most leaves the chlorophyll is homogeneously scattered; but in a few plants with variegated leaves, like *Begonia sanguinea*, *Peperomia blanda*, &c., it is isolated in particular spots. The leaves of orchids show three types of structure: 1. Like ordinary leaves; 2. With collections of spiral cells in the parenchyma, which is green throughout its thickness; 3. With a middle layer of green cells, separated from either layer of epidermis by a layer of colourless cells,—but more often there is only a single layer of colourless cells inferiorly with spiral cells, while the parenchyma under the upper epidermis is composed of seven or eight layers of cells, of which some only are spiral. There are several other less important modifications of structure in other plants, and for a description of these the student is referred to the exhaustive memoirs of Brongniart[1] and Trecul.[2]

Succulent Plants.—In fleshy plants like the Cactaceæ, stone-crops, aloes, &c., there is a great amount of water contained in the parenchyma of the leaves. This is not, however, owing to absence of stomata, but to the thicker epidermis, or to the deposit which forms in the infra-epidermal cells. The stomata are usually abundantly scattered over the epidermis of these plants, but except in young and growing parts, seem to open less than in ordinary

---

[1] Ann. des Sc. Nat., 1e sér. t. xxi. (1830).

[2] Bull. Bot. Soc. Fr., ii. 448 (1855).

plants. The result is, that the tissue is gorged with sap during the hot season when it is required by the plant, which retains it with great tenacity. Hence such plants are well suited for resisting great droughts, as seems evinced by the fact that they inhabit arid places, where the sun's rays beat down with a rigour unabated by any modifying circumstances of shade. Thus we find Cactaceæ in the torrid Colorado desert, and the *Tierra caliente* of Mexico; Stapelias, Aloes, and Euphorbias in the sandy African wastes; or still more familiarly, the ordinary stone-crops (*Sedum*) and houseleek (*Sempervivum tectorum*) prospering in places where they can receive but little moisture. Yet, by economising what they receive, they live and prosper where others perish. The drier the atmosphere, the more unwilling are succulent plants to part with their moisture; hence they can live in our rooms, where the air is much drier than outside: and for this reason ferns and other plants which part easily with moisture do not grow readily, unless continually watered, unprotected in rooms where there are fires, or the atmosphere of which is very dry. (*See* TRANSPIRATION, chap. v.)

Structure of the Leaves of Water-Plants.—In the leaves of plants which either float on or are submerged in water, we find an interesting modification of structure to suit their peculiar mode of life. As already remarked, with a very few exceptions there are no stomata on the under surface of floating leaves, or on either surface of submerged leaves. The thin epidermis, however, serves the purpose of transpiration and respiration. In some submerged leaves, though the nerves are present, they lose their vessels, such being no longer needed for the purposes of nutrition of plants submerged in their medium from which they draw their food; while it often happens (as in *Trapa natans*, water-caltrops, *Ranunculus aquatilis*, water-crowfoot, &c.) that the nerves of the submerged leaves are left free without any intervening parenchyma, and look like roots floating in the water.

In the leaves of nearly all water-plants (fig. 97), and remarkably so in the huge ones of *Victoria regia*, there are large air-cavities, with, however, no direct communication with the exterior.[1] In *Zostera marina* (fig. 96), and other *Naiadaceæ*, there are nerves without vessels, these nerves being arranged in equal parallel lines connected by transverse branches, with a row of cells superiorly not unlike the "palisaded cells," but without epidermis; and contrary to what we find usual in land-plants, this infra-epidermal layer is gorged with chlorophyll. In *Potamogeton* (ordinary pond-weed), *Zannichellia* (horned pond-weed), &c., there is no derma, only a cuticle (p. 52) of excessive thinness, and no woody bundles; but

---

[1] Such lacunæ are also seen in the *stem* of some marsh-plants—as, for example, the beautiful structure seen in the aerial stem of *Hippuris vulgaris*, the common "marestail."

these are replaced by a series of elongated cells which take their place.

In *Utricularia* (order Lentibulariaceæ) we have another arrangement for floating the plant. Small *ascidia* or sacs[1] (figs. 99, 100) are connected with the leaves, which, about the time of flowering, are filled with air, and buoy the plant to the surface. The structure is shown in our figures. These ascidia are probably, from their axillary situation, to be looked on as modified branches (Schacht); or, according to some (Schleiden, Göppert, Benjamin), as a part of the leaf itself. The opening of each sac is surrounded by forked hairs composed of four cells, and is closed by a transverse cellular membrane, like the valve of a pump, capable of opening from without inwards, and which resists when it is pressed from within outwards (Benjamin). The walls are composed of from 2-4 layers of cells, bag-cavities between which establish a communication with the interior of the sac and the outside air, the mouths of such openings being guarded by cells analogous to the stomata. Göppert has found in the interior layer of cells a blue matter somewhat analogous to that found in flowers. The physiological function of these ascidia is full of interest. At first they are filled with a somewhat gelatinous liquid, which by its weight assists in retaining the plant at the bottom of the water. Very soon the branching hairs already described, which project into the interior, secrete a gas which accumulates as the gelatinous substance diminishes. By-and-by, when the vessels are full, the plant gets light and buoyant, and disengaging its roots from the soil, rises to the surface of the water and flowers. The flowering over, and the fruit mature, the air disappears from the ascidia, the valve allows the water to enter, and again the plant sinks to

Fig. 99. — Fragment of the stem of *Utricularia vulgaris*, L. *t' t'* Subdivided branches, each bearing several leaves, and the ascidia *tu*.

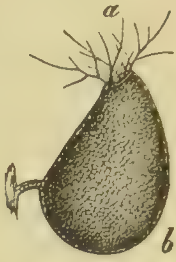


Fig. 100.—An ascidium of *U. vulgaris*, complete on its pedicel. *b* Its wall, externally much swollen; *a* filaments which surround its opening (magnified).

---

[1] ᾿Ασκός, sac; also called *ampullæ* (Bischoff).

the bottom, to remain there until spring stimulates its ascidia again into activity. Altogether, the physiological history of the *Utricularia* (or "bladderwort," of which we have three species in Britain) is one of the most beautiful we can meet with in vegetable biology.[1]

In some other plants, such as *Pontaderia crassipes*, Mart., of Brazil, *P. azurea*, of South America, and *Trapa natans*, the petioles of some of the submerged leaves are dilated into air-cavities which act as floats. The submerged leaves of the latter plant consist simply of ribs floating free without parenchyma (as in other plants, p. 173), while the leaves in contact with the air are of the ordinary structure. A somewhat analogous structure to the inflated petiole of *Trapa natans* is found in the fistulose leaves of *Allium*, *Lobelia*, *Dortmanna* (divided into four cavities), &c. In the lace-plant of Madagascar (*Ouvirandra fenestralis*), there is an open network all over the floating leaf, formed by the absence (or rupture?) of parenchyma within the meshes of the network of veins; while in *Monstera Adansonii*, Schott,[2] there are in the leaf distinct holes, oval or oblong, directed more or less obliquely to the side, and from 2 to 4 centimetres in size. The parenchyma is, however, continuous in the young state of the leaf. The changes have been very lucidly described by Trecul. Lacunæ appear in the centre of the *mesophyll*, the cells round which lacunæ become colourless, and multiply so as to form walls to them. After a short time gas accumulates in the lacunæ, which puffs out the superior, and by-and-by ruptures the inferior epidermis; the superior epidermis soon goes also, and the apertures are complete. Such leaves are styled *fenestrate*.[3] If a plant of *Marsilia quadrifolia* is sunk beneath the water, Hildebrand has shown that the growing leaves will elongate their petioles even to the extent of three feet, to allow the leaves to reach the surface.

DEVELOPMENT OF LEAVES.

(1.) The first appearance of the leaf is in a minute more or less elongated parenchymatous and exceedingly delicate point, produced at the extremity of a stem or branch while in full vital activity in spring. This constitutes the growing point.

(2.) After some time there appear little projections or papillæ of cellular tissue on its sides. These are the future leaves. Then

---

[1] *Vide* Duchartre, lib. cit. p. 300. I give the above facts on his authority, not having seen Göppert's or Benjamin's papers, nor having been able to repeat their observations at the date of writing.

[2] *Dracontium pertusum*, L.; *Scindapsus pertusus*, Sch.; *Pothos repens*, H. P.

[3] *Fenestra*, a window.

the central cells in the middle of the papillæ begin to elongate, and so form the veins, which at first consist of tracheæ and annular vessels. At the same time the papillæ rise little by little outwards, and in due course take a definite form, until each has assumed the form characteristic of the leaf of the particular plant it is found on, or the particular part to which such a leaf is proper. This development of the leaf, briefly sketched in a few words in the preceding paragraph, takes place after two main types—viz., the *basipetal*[1] and the *basifugal*[2] methods. Let us explain these somewhat more in detail. In the "basipetal" method of development, the portion of the papillæ which first appears is what afterwards constitutes the summit of the leaf: this does not afterwards increase much, the additions to it being made by the base, while the leaf is gradually pushed further and further out of the axis on which it grows. On the contrary, in the "basifugal" development, the active forces by which the leaf is formed reside in the superior part of it. Accordingly, the new tissues are there formed, and the portions at the base are oldest, while those at the summit are the newest. This is a much rarer type of development than the former.

Appearance of the Leaflets and Lobes.—Take any compound leaf—that of the rose, for example—and we see arising from the axis an elongated cellular body which is the common petiole. Smaller papillæ appear on either side; these are the leaflets. If the leaf is of the basipetal type, the odd lobe is an imparipinnate leaf, and the upper ones generally are first formed, and are always further advanced than those lower down. This is also the case in some digitate leaves. However, in the walnut and other large compound leaves of that nature, the formation proceeds from below upwards, and new leaflets are formed at the apex after the lower ones are fully blown. The pinnate leaves of most leguminous plants (*Galega*, false acacia (*Robinia Pseudacacia*), *Mahonia*, &c.) are also of the basifugal type. All leaves are at first entire; the lobulation and other divisions of the margin appear subsequently, and follow a similar law of development to that of the leaf itself.

It thus appears that in some simple leaves the upper portion, and in some compound leaves the upper leaflets, appear first; and that in others this order of development is reversed,—these two types constituting respectively the *basipetal* and *basifugal* methods of leaf-development.

Appearance of Stipules, Sheaths, and Petioles.—It has been asserted by Mercklin and others, that the limb of the leaf and the summit of the petiole are developed before the stipules and the inferior part of the petiole. Trecul and Schacht have, however, shown that this is incorrect, and that the stipule, when present,

---

[1] Basim patens.

[2] Basim fugens.

is early developed, even before the papillæ which form the future leaflets, or the lobes, have made their appearance. It often, however, falls off or gets arrested in development in an early stage, especially among plants of the order Cruciferæ (p. 150). When there is a sheath it always shows itself first; and, lastly, the petiole appears — in simple leaves, after the limb has attained some size, but, in compound leaves, before any of the leaflets have appeared; since, as we have already seen, it is the common petiole from which these leaflets spring on either side. Once formed, however, the petiole elongates rapidly, especially in the upper portion. However, in some cases it is almost stationary at the base, while the upper portion develops rapidly. The same law holds true in regard to the formation of the ribs and veins, and their ramification through the parenchyma. The sheath in most monocotyledons, and the stipules, are at first continuous with the blade, only separated by a constriction, but they are afterwards separated from it. The stipules remaining near the axis develop rapidly, and are often larger than the leaves, and, as in the case of the maple, form the covering for the young leaf.

These two types (the basipetal and the basifugal) of development may be mixed—*e. g.*, when the lobes commence from above downwards (basipetal), and the veins ramify from base to summit (basifugal); but as these are only modifications of the two main types, it is unnecessary to enter into a further consideration of them.

Lastly, the stomata make their appearance in the manner already described (p. 55).[1]

LEAF-BUDS.

Leaf-Buds are like ordinary buds (p. 74) ovoid or elongated, generally pointed at the summit, and are produced either at the extremity of the stem or branch, or more commonly in the axil of

---

[1] A much more elaborate and somewhat different account of the development of the leaf has been given by Eichler and others. At the same time it is very complicated, and therefore as much calculated to confuse as to instruct the student, however valuable it may be to the more learned botanist. After paying some attention to the subject, however, I am not certain that it is any improvement on the older account, unless an infinitude of new technical names be taken as such. See Eichler's Zur Entwickelungsgeschicte der Blattes, 1861; and a summary, with additional notes, by W. R. M'Nab, in Trans. Bot. Soc. Edin., 1865-66; Steinhul in Ann. des Sc. Nat., 1837, viii. 257-304; Mercklin Zur Entwickelungsgeschichte der Blattgestalten, 1846 (and Abstract in Ann. des Sc. Nat., 1846, vi. 215-246); Trecul in Ann. des Sc. Nat., 1853, xx. 183-190; Schacht, Lehrbuch, t. ii. (1859), sec. 104 *et seq;* Wretschko, Sitzungsberichte, &c., 1864, s. 257-280, &c.

the leaf, in the manner described, and become prominently marked when the leaf falls, the bud being then ready, when the spring comes, to take its place. The bud has sometimes been compared to an embryo, but it differs essentially from an embryo in so far that it cannot produce a new branch or leaf unless attached to a living stem. Most frequently in temperate countries the bud is covered with scales,[1] — these scales in their turn being often covered with a resinous substance,—the whole serving to render it impervious to moisture, and to protect it against cold. In tropical countries naked buds are not uncommon: the black-thorn (*Rhamnus Frangula*) affords a rare example of such in this country. These protecting covering scales are, in most instances, various organs arrested in their development; in some cases they are leaves, stipules, or even the persistent bases of preceding leaves. When the bud, as in the case we have more particularly to deal with just now, contains the young leaves, it is called a leaf-bud; if it contains the young flower, it is a flower-bud. The bud, as the growing point of the stem, we have already adverted to in our account of that portion of the plant; while the turio, bulb, and bulbule we have already classed, for the sake of convenience, among the forms of underground stems, though in reality they are modified buds.

PRÆFOLIATION.

Præfoliation, or as it is sometimes—though somewhat unmeaningly—called, by Linnæus's term, *Vernation*, is concerned with the different ways the young leaf is arranged inside the bud. We may view this in two lights,—viz., 1st, the way in which the individual leaf is folded on itself; and 2d, the way all the leaves inside the bud are arranged in reference to each other. This is not the same in every species of plant. Therefore, in reference to the first relation, we may class the different ways leaves are folded under seven different heads, as follows:—

A. FOLDED LEAVES.

1. *Conduplicate* (fig. 101)—folded from the midrib, so that one half is applied by its upper surface to the other half. *Ex.* Oaks, Magnolia, Almond, Syringa (*Philadelphus coronarius*).

2. *Reclinate* or inflexed—when the apex is bent to the base. *Ex.* Tulip-tree (*Liriodendron tulipifera*), Aconite (*Aconitum Napellus*).

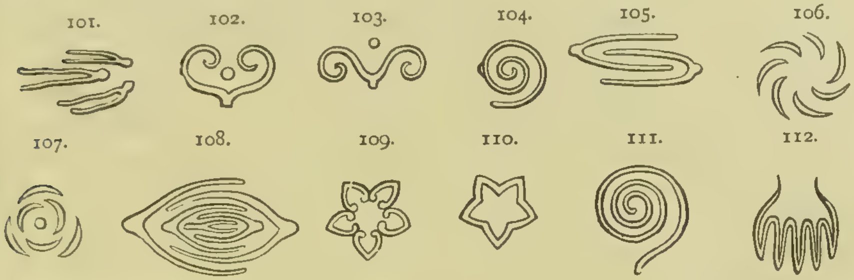
3. *Plicate* or plaited (fig. 112)—when folded like a fan. *Ex.* Vine, Maple, Gooseberries.

---

[1] *Tegmenta* or *perulæ*. Buds are the *hybernacula*, or winter-quarters, in the somewhat romantic nomenclature of Linnæus (p. 74).

B. Rolled Leaves.

4. *Convolute* (fig. 104)—when rolled from one edge in a single roll. *Ex.* Apricot, Plum, Barberry, *Arum.*



Figures showing the different forms of præfoliation. Fig. 101, conduplicate. Fig. 102, involute. Fig. 103, revolute. Fig. 104, convolute. Fig. 105, demi-equitant. Fig. 106, twisted. Fig. 107, imbricate. Fig. 108, equitant. Fig. 109, induplicate. Fig. 110, valvate. Fig. 111, circinate. Fig. 112, plicate.

5. *Revolute* (fig. 103)—when each edge is rolled outwards from the midrib. *Ex.* Rosemary, Azalea, Sorrel.

6. *Involute* (fig. 102)—when each edge is rolled inwards towards the midrib. *Ex.* Water-lily, Violet, Poplar, Bean, Honeysuckle.

7. *Circinate* (fig. 111)—rolled at the top in the manner of a crosier. *Ex.* Ferns, Sundews (Drosera), *Pilularia.*

In addition to the two great classes given, M. Clos has established three others,—viz., those with plain vernation, those with cylindrical vernation, and those with crumpled vernation; all of these classes, however, merge by various transitions one into the other.

As regards the way leaves are arranged in the bud in relation to each other, five classes may be noted :—

A. Straight Leaves.

1. *Valvate* (fig. 110)—when they touch each other simply by their contiguous borders.

2. *Induplicate* (fig. 109)—when the outer successively overlap the inner ones, by their edges at least. In this case the phyllotaxis is exhibited in the order of overlapping.

3. *Imbricate* (fig. 107)—when the outer leaves overlap the interior ones more or less by their sides. *Ex. Lilac,* Laurel, Ash. *Twisted* or spiral (fig. 106) is only a modification of this.

In the above three forms of præfoliation the leaves were tolerably straight or convex, and not doubled on themselves. In the next two forms, however, we find the opposite arrangement.

B. Leaves Folded in Two. (Conduplicate.)

4. *Equitant* (fig. 108)—when they successively embrace each other. *Ex.* Iris, Privet.

5. *Demi-Equitant, or Obvolute* (fig. 105)—when only one-half of

a leaf embraces one-half of another. *Ex.* Sage (*Salvia officinalis*), Scabiosa, Pink.

The same names are applied to the full-grown leaves when they are so situated as to necessitate such names being applied, as when they embrace or overlie each other. Under the name of æstivation or præfloration, these names are also applied to the parts in the flower-bud.

Some plants, like the *Magnolia*, *Duvaua*, *Isatis*, *Rheum*, *Cupuliferæ*, &c., have a double præfoliation. Etiologically, the præfoliation is often determined by a contraction or constraint caused during the period of the development of the limb. Some orders, related to each other by natural affinities, show a uniformity in their præfoliation, and all the members of many orders have equally a uniform præfoliation—*e.g.*, *Iridaceæ*, *Hæmodoraceæ*, *Hypoxidaceæ* (Amarillydaceæ)—with conduplicate prefoliation; *Scitamenaceæ*, with convolute præfoliation; *Malvaceæ*, conduplicate; *Hippocastanaceæ*, conduplicate; *Verbenaceæ* and *Globulariaceæ*, conduplicate; *Leniceraceæ* (Caprifoliaceæ), involute; *Cornaceæ* and *Garryaceæ*, also involute, &c.

Again, while a number of orders and families have a single kind of præfoliation, there are others which show two, three, four, and even, as in the case of the *Labiatæ*, five types. Certain anomalous types in certain families are also distinguised by peculiar præfoliation—*e.g.*, the genus *Podophyllum* among the *Berberidaceæ*, *Ginkgo* among the *Coniferæ*, *Funkia* among the *Hemerocallideæ* (Liliaceæ), *Fabiana* among the *Solanaceæ*, &c. *Acorus* has three modes of præfoliation in the species composing the genus; *Allium* four,—and so on. Præfoliation is, however, often useful to coordinate doubtful genera and species.[1]

VENATION.

The forms of leaves are almost infinitely various, but in most cases the leaves of each species keep certain determinate forms, which, in common with other characteristics, are useful in the characterisation of the species. The names applied to leaves are for the most part arbitrary, and derived from a supposed or real likeness to some natural, artificial, or other object. Until recently there was no philosophical account of the laws of structure regulating the formation of these variedly outlined organs, and, accordingly, to remember the numerous names applied to the different kinds of leaves was a tedious task on the student's

---

[1] Clos., Monographie de la préfoliation (Mem. de l'Acad. Imp. des Sc. de Toulouse, 7e ser. t. ii. 91-134, 1870), and Bull. Soc. Bot. Fr., 1870, p. 122, 123.

memory. De Candolle has, however, considered that these forms may be reduced to a few types, dependent on the different forms and reticulations of the midrib and veins. The student will, however, have already seen that, though this theory is useful as an aid to memory, it will not explain the *form* of the leaves, for the parenchyma is developed in the vast number of cases before the midrib is formed. De Candolle's theory will only "account for the mutual adaptation and correspondences of outlines and framework." Viewing it in this light, we shall now explain the main points of it, commencing first with the venation, or *nervation*, as it is sometimes called.

The *veins* are the subdivisions of the petiole, forming the framework of the leaf. (1.) In a typical dicotyledonous leaf like that of the elm, for example, the petiole is continued straight up into the laminæ, attenuating near the type, and dividing the leaf in two equal parts. This middle branch is called the *midrib.* (2.) On its passage upwards the midrib gives off *ribs* or *nerves* properly so-called. (3.) These ribs in their turn give off other smaller ones, called *veins;* and (4.) finally, these give off others which constitute the final subdivision of the petiole, and which by their anastomosis form the fibrous network of the leaf—viz., the *veinlets* or little veins. Though these terms are applied, the student must remember that in reality the subdivisions of the midrib have no connection of the most distant character with nerves, and hardly more with veins.

The *Venation* presents various primary modifications—

(1.) Either the vessels composing the petiole divide at once when they enter the blade into several veins which run parallel to each other to the apex connected by simple, feeble, transverse veinlets; or,

(2.) The petiole is continued into the blade, in the form of one or more principal or curved veins, which send off branches on either side—the smaller ones anastomosing with one another in a kind of network.

The first is the great division of *parallel* or *curved* veins characteristic of the great division of plants called *Monocotyledons* or *Endogens;* the second is the *reticulated* or netted (or angular-veined) veined leaves equally characteristic of the *Dicotyledons* or *Exogens.* In Ferns, again, there is an intermediate variety of venation—viz., the *furcate* or forked. There are, however, a few exceptions, as we shall by-and-by see, though for all practical purposes the rule as given may be taken as general.

The minor modifications of venation depend upon the more or less marked character of the veins, on the greater or less thickness of the interposed parenchyma, or the number of vessels composing the veins, and on the method in which the secondary veins or ribs are given off from the primary one or midrib, which is simply a continuation of the petiole. We can detect four types in which the ribs are given off from the midrib :—

(1.) *Pinninerved* leaves, in which the ribs are given off on either side of the midrib at an acute angle, like the pinnæ on a compound leaf.

(2.) *Palminerved* leaves, in which the midrib divides at the base into 3, 5, 7, or a greater number of strongly marked divisions, nearly as thick as the midrib itself, the whole bearing a rude resemblance to the palm of the hand with the fingers extended. A good example is seen in the leaves of ivy, maple, gooseberry, and mallow.

(3.) *Peltinerved leaves*, in which the petiole enters the leaf at or near its centre, and gives off veins in a radiating manner.

(4.) *Pedinerved leaves*. This is seen in most composite leaves, such as those of *Dracunculus vulgaris*. Here the petiole divides at entering the leaves into three main divisions. The middle one, or the continuation of the petiole, is in general feeble, and supplies a single segment; the other two come off at right angles at the base of the first, and are much more strongly marked. Each of these splits into two divisions, the upper division of each supplying a leaflet, while the under division splits into three or more to supply as many secondary divisions of the compound leaf.

Very frequently the midrib is not present. Sometimes the veins go straight to the margin, as in the beech and chestnut; while in others, they are divided into veinlets long before coming to the margin.

When the midrib gives off a very strong primary vein on each side just above the base, as in the sunflower, it is said to be *triple-nerved;* if two are given off on each side, *quintuple-nerved*, or ribbed.

Occasionally they converge to the apex, looking like parallel veins; but they are not so, as the intermediate small netted veins show. "Nerved," it may be remarked, is often applied to ribs when not prominent or strong, though they may branch before reaching the apex.

Normally, the veins never appear at the surface unless it may be in the form of the spines on the edge of the leaves of various plants, such as the holly. However, in an abnormal condition of this latter shrub, they appear in the form of prickles on the upper surface of the leaf, constituting the cultivated variety known as *Ilex Aquifolium ferox.*

Correspondence between Venation and Ramification.—Principal M'Cosh and Professor Dickie consider that they have traced some connection between venation and ramification; and certainly there seems something more than mere coincidence in the numerous examples they quote in support of their ingenious and interesting speculations. The following are some of the chief laws which they consider they are justified in asserting as having been made out :—

(1.) In plants with woody structure there seems to be a correspondence between the tree and the leaf in this respect,—that a leaf without a petiole implies a trunk naturally branched from the ground ; and a leaf with a petiole implies that the species of tree on which it grows has naturally a bark trunk. *Ex.* Beech.

(2.) There is a correspondence between the disposition and distribution of the branches and the disposition and distribution of the leaf-veins. *Ex.* Beech, Poplar, &c.

(3.) There is a correspondence between the angle at which the branches go off, and that at which the lateral veins go off. In most plants with a woody structure, the angle of both vein and branch is between 45° and 60°. In the greater number of herbaceous plants, it varies between 25° and 45° ; but both in trees and herbaceous plants there are angles as acute as from 10° to 15°, and so obtuse as 70° or 75°.

(4.) There is a correspondence between the curve of the veins and the curve of the corresponding branches.[1]

Of late years much attention has been paid to the venation of leaves, with a view to finding characters to distinguish various species of fossil plants. More especially have fossil ferns been studied from this point of view by Brongniart, Presl, Gaudichaud, &c. ;[2] and the same attention has been paid to this, and with marked success, by Ettingshausen, Pokorny, Von Buch, and more especially by Oswald Heer, in the determination of the species of tertiary plants. The late Professor Oersted, of Copenhagen, has also applied the venation to the classification of Cupuliferæ.[3] It has been positively affirmed that though a large number of the Umbelliferæ have a venation like the rest of Dicotyledons, yet that about one-half of them there is a peculiarity in the existence of a vein at the very edge of the leaf itself, and which more or less entirely fringes its whole margin. The venation of the umbelliferæ—a puzzling order to determine the species of—is very variable in different species, " but constant and highly characteristic in each species." [4] As a rule, however, the leaf is too variable to use as a character for species.

---

[1] Typical Forms and Special Ends in Creation, p. 111-123, and the Rev. Dr Macmillan's Foot-Notes from the Page of Nature, for a discussion on some similar points in vegetable morphology.

[2] Dr Hooker has, however, shown that it is impossible to distinguish fossil ferns by their venation only (Mem. Geol. Survey of Great Britain, vol. ii. part 2, p. 387).

[3] Bidrag til Egeslægten Systematik. (Nat. Forening Vidensk. Meddelser, 1866, p. 1-96), &c.

[4] Gorham, Quart. Journ. Mic. Sc., 1868 (No. xxix. n. 3), p. 25.

FORMS OF LEAVES.

According to De Candolle's theory, the shape of the leaf may be viewed as dependent on the distribution of the veins, and the quantity of parenchyma scattered through their interstices—the general outline being determined by the divisions and direction of the veins, by the greater or less abundance of parenchyma, through the midst of which the veins are distributed. This proceeds on the assumption that the blade is an expansion of parenchyma, in which the former veins are ramified.

For example, if the principal veins of a pinninerved or feather-veined leaf are not greatly prolonged, and are about equal in length, the leaf will be more or less elongated; and if, in addition, the ribs given off from the midrib are very short in proportion to the midrib, the leaf is *linear;* if they are longer in proportion, the leaf will be oblong, which a slight rounding of the edges converts into an *oval* or *elliptical* outline. If the veins near the base are the longest, and especially if they curve towards their extremities, the edge is *lanceolate* or *ovate*, or some intermediate form. But if they are developed beyond the middle of the blade, the leaf becomes *obovate* or *cuneiform*,—and so on.

Again, many leaves have a sinus or rounded incision at the base, which, according to this theory, is produced by the ribs or their ramifications being directed backwards—producing the *reniform* leaf. When the two sides of such a leaf come together, the result is an *orbicular* or peltate leaf. When the veins run parallel (as in grass), the leaf is necessarily linear; but if they diverge, the result is an oval form, or some modification of that form.

[For a tabular synopsis of the different forms of leaves, see p. 202.]

Margin.—The margin is *entire* when there are no breaks in it whatever. According to De Candolle's hypothesis, notches, serrations, &c., are owing to an insufficiency of parenchyma to fill up the outline. Hence the sub-aquatic leaves of *Ranunculus aquatilis* (*e.g.*), which are said usually to be "foliformly cut," are in reality only the skeleton of the leaf without any intermediate parenchyma to fill up the interstices; while in the other leaves—aerial leaves of the same species—there is a sufficiency of parenchyma, the result of which is that these are only lobed. However, as we have already seen, though this hypothesis of De Candolle is useful as an aid to some more philosophical classification of leaf-forms, yet the parenchyma, and therefore the outline of the leaf, being formed before the vein, it is in reality untenable in a strictly scientific aspect.

According to his hypothesis, monocotyledons being parallel-veined, would necessarily have entire leaves, while dicotyledons would in most cases have the margins of their leaves divided. In reality this is what we find in most cases in these two great divisions of plants.

The extent of the division of the margin is expressed by the adjectives, dentated, serrate, crenate, &c. [*vide* table on p. 206]. If the indentations are deep, the leaf is *fissured;* if shallow, *lobed;* if the division is deep, rounded, and generally acting as the division between the two sides of the leaf, it is called a *sinus.* Leaves divided by fissures are in general described by the affix *fid.* Hence (*e. g.*) a leaf which presents a number of deep, almost symmetrical fissures on both sides of the midrib in a feathery manner, is called *pinnatifid*—that is to say, the lobes resemble the leaflets of a pinnate leaf. If the divisions are still deeper, the lobes are then called *partitions* (De Candolle), and the leaf is *partite.* This designation entering in the formation of composite words, is used to designate the particular form of leaf. Thus, if a leaf is divided on the edges like a pinnatifid leaf, but more deeply, it is called *pinnati-partite.* Finally, when the margin of the leaf is cut up in an irregular manner, and so deeply that it is with difficulty that the original form of the leaf can be traced, it is called *dissected*—this word also entering into compound adjectives like the other. Thus we qualify a leaf as *pinnati-sected* when it is divided on the plan of pinnatifid and pinnati-partite leaves, but much more deeply. All these terms, as well as those applied to the apex or base of the leaf [table, p. 203], are equally applicable to petals, sepals, &c., and many of them are also applicable to the stem and stalk.

COMPOUND LEAVES.

Hitherto all that we have said has related to *simple* leaves; or, in other words, leaves in which the vascular bundles composing the petiole expand out into one blade alone, and in which, if there are divisions, these divisions are not articulated to the midrib or to the petiole by their own petiole, but are all one piece (fig. 111). On the contrary, in *compound leaves* (fig. 113), the vascular bundles expand in several blades, distinct one from the other, which form leaflets, united by their own petioles to the common petiole. There are, however, transitions from the one type to the other. Compound leaves may again be divided into two great divisions—(1.) *Pinnate*, and (2.) *Palmate* or Digitate leaves.

1. **Pinnate Leaves.**—In these leaves (fig. 113) the leaflets or pinnæ are arranged along the two sides of a common petiole, by secondary petioles (or *petiolules*). After a number of pairs of leaflets have been borne along the sides of this common petiole, the common

leaf may end in an odd one—the leaf is then said to be *imparipinnate*, as in the vetch tribe; or the leaf may end abruptly, terminating in two leaflets, as in the common garden-bean (*Faba vulgaris*), when the compound leaf is said to be *abruptly* or *paripinnate*. An imparipinnate leaf is said to be trifoliate or ternate when it is composed of a single pair of opposite leaflets, and terminated by an odd leaflet (as in the haricot bean). The degree of subdivision does not end here. Not only does the common petiole bear leaflets, but secondary pinnate petioles, which in their turn give attachment to leaflets arranged on them. Such leaves are called *bipinnate*, as in the common sensitive plant (*Mimosa pudica*). A number of plants are even more compound than that, since their primary petiole divides into secondary petioles, which in their turn bear tertiary lateral petioles; and it is only on these, however, that the pinnate leaves are borne. Such leaves are thrice pinnate or *tripinnate*, or *decompound*. They may be even *supra-decompound*, or still further subdivided. Pinnate leaves may be composed of a greater or less number of leaflets. The leaflets, again, may be *opposite*—*i. e.*, in two's opposite to each other (*opposite-pinnate*), or alternate (*alternati-pinnate*). In opposite-pinnate leaves (which are also often called *conjugate* leaves),

Fig. 113.—Imparipinnate leaf of the false Acacia (*Robinia Pseudacacia*, L.)

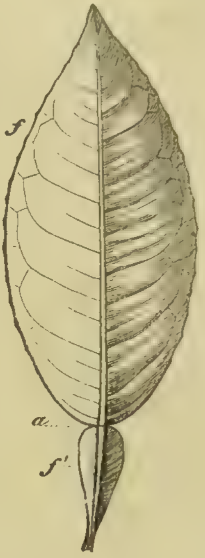


Fig. 114.—Compound unifoliate leaf of the Orange (*Citrus Aurantium*, L.) *f* Lamina; *f'* Petiole, winged on either side; *a* Point of union of the two, marked by an articulation.

the number of leaflets arranged along the common petiole may be variable; while the words *unijugate*,[1] *bijugate*, *trijugate*, *quadrijugate*, and *multijugate*, express whether there is one, or two, three, four, or a greater number of pairs of leaflets.

Fig. 115.—Plant which chiefly yields the gum-arabic (*Mimosa Arabica*); flowering branch (*a*) and fruit (*b*). The leaves are bipinnate.

2. **Palmate, or Digitate Leaves.**—In this form of leaf the leaflets radiate from the summit of a common petiole, and from its resemblance to the hand,[2] or outspread fingers,[3] it derives the two names it is equally known by. The leaf of the horse-chestnut (fig. 116) is a good example. In a palmate leaf there may be a variable number of leaflets. Thus, in the trefoil or clover (*Trifolium pratense*), and *Hedysarum gyrans*, there are three (*digitately-trifoliate, alternate*[4]); in *Pavia* five (*digitately-quinquefoliate*); seven

---

[1] *Unum*, one; *jugum*, a yoke.

[2] *Palma*, the palm of the hand.

[3] *Digitus*, a finger.

[4] It is sometimes not very easy to say whether a leaf is trifoliate or only imparipinnate, when, as in the latter case, there happen only to be two side leaflets, and the odd one terminating the common petiole. However, if on examining the attachment of the odd leaflet it is found (as in the clover) to be

(*digitately-septemfoliate*) in the horse-chestnut (*Æsculus Hippocastanum*); or, as in some species of lupin, a great number (*digitately-multifoliate*).

Fig. 116. — Compound digitate leaf of Horse-chestnut (*Æsculus Hippocastanum*).

Digitately-peltate Leaves.—De Candolle has applied the name of compound peltate leaves to the leaves of *Sterculia fœtida*, and a few other suchlike. Examine the figure of the peltate leaf at p. 202 (fig. 128), and suppose that each of the radiating nerves was replaced by distinct separate leaflets, then we would have such a leaf as that which we have indicated.

Digitately-pinnate Leaves are those in which the secondary petioles, as in some Mimosas, bear secondary leaflets, thus simulating pinnate leaves. In *Bigeminate* leaves each of the secondary petioles bears a solitary pair of leaflets. (*Ex.* Mimosa ungius-cati).

In *Bipinnate* leaves of the palmate type, each of the secondary petioles bears pinnæ along its sides, just like ordinary pinnate leaves. *Ex.* Mimosa julibrizin.

Finally, cases occur in which the secondary petioles divide into tertiary petioles bearing leaflets. Or a case may be in which the common petiole divides into three secondary petioles, each divided into three tertiary petioles, bearing each their leaflets, as in *Actæa spicata*, *Epimedium alpinum*, &c. The leaf of the citrons and oranges (fig. 114)—an order of which all the other members have compound leaves—might seem at first sight simple; but on examining it closely, there is seen an articulation at *a*, by which the single blade *f* attaches itself to the petiole *f'*, which is marked by two winged foliaceous expansions on either side. This may be said, therefore, to be a pinnate leaf, the lateral leaflets of which have become abortive, since only the odd terminal leaflet remains, but which, by way of compensation, has taken a considerable development. There is something analogous also seen in some leguminosæ. Such a leaf may be called a *unifoliate compound* leaf.

from about the same level as the two side leaflets, it may be safely pronounced to be a *trifoliate* leaf; if, on the contrary, the odd leaflet (as in fig. 111) is much above the point of attachment of the side ones, then little doubt need remain regarding the *pinnate* character of such a leaf.

Succession of Compound and Simple Leaves.—Some plants produce at first compound, and then at a subsequent stage simple leaves, or reciprocally. For instance, Dr Geo. Lawson showed that the common gorse or whin (*Ulex*) at an early stage gives birth to a dozen or twenty leaves, provided each with three leaflets, but by-and-by it commences to produce spines, while simultaneously the leaves are reduced to simple little scales. On the other hand, in certain Australian *Leguminosæ*, the stem bears at first simple leaves, which give place by-and-by to compound ones, after the stem has grown considerably.

Variability of Leaves.—Finally, it ought to be added, that the leaves on some plants are very variable, according to their position on the stem or branches, as may be seen by examining a plant of ivy or a bush of holly. In the ivy, for instance, the leaves in the vicinity of the flowers are differently shaped from the ordinary ones, in so far that they have no lobation at the margin or cleft at the base, and become nearly twice as long as broad. In the "snowberry" (*Symplocarpus racemosus*) of North-west America, the first leaves produced on the branch are undivided. However, as the vegetative energy increases, the next leaves produced become more or less cut on the edge, the next less, until, finally, when the year's growth is completed, the uppermost of all are entire. (See also fig. 115.)

In *Broussonetia papyrifera*, out of the pith of which paper is made, and out of the liber of which the Polynesians weave their cloth, Duchartre notices the extreme diversity of the leaves, from being perfectly entire to deep lobation. Again, in the water-crowfoot (*Ranunculus aquatilis*), we see the upper leaves entire, and the lower ones, which are immersed in the water, so divided as to be reduced to nerves without parenchyma. The same appearance is seen in *Cabomba oblongifolia*, another water-plant, &c. (p. 159, 168). In *Laurus Sassafras* some leaves are entire, others two-lobed, and others three-lobed, even on the same branch, according to the height they are placed on the stem or branches. In *Gleditschia triacanthus*, the pinnately compound leaves, instead of having, as is usual, only a single leaflet borne on each petiolule, have occasionally on each petiolule several little leaflets; in other words, the leaflets become themselves compound.[1] The proportion between the different parts of the leaf also sometimes varies according to the position of the leaf on the stem. Thus, in general, the sheath—when this is present—is more developed than the blade in leaves placed at the base or at the summit. Leaves will also often be entire, repand, crenate, or serrate, on the same plant, as seen in the common holly; and in some North-west American oaks (*Q. agrifolia*, &c.), one side of the leaf may be dentate, and the other entire.[2]

---

[1] Payer, Eléments, &c., p. 36.

[2] See my Horæ Sylvanæ, p. 72.

Phyllomorphosis.—The study of the succession and variation of leaves during different seasons has received some attention of

Fig. 117.—Plant of *Campanula rotundifolia*, L., showing the difference between the configuration of the radicle leaves *f f*, and the others *f'*.

late years—chiefly by Schleiden, Braun, and Rossmann—and has received the name of *Phyllomorphosis.* They consider that all the variations of leaves may be traced to—(1.) alterations in the form of the limb ; (2.) alterations in the form of the petiole ; or (3.) dependent on the two parts developing equally. The *basilar* leaf, or that which in most monocotyledons, and in a few dicotoyledons (strawberries), first appears on the branch, and is distinguished from those which follow by being small, thin, membranous, pale, and most often placed on the inner side of the branch, the Germans have called *vorblatt*, and the French (Gay) *préfeuille*. It may be translated into Latin as the *præfolium*, and seems destined to act as a shelter to the younger parts found below it.[1]

ANOMALOUS FORMS OF LEAVES.

Unsymmetrical Leaves.—In most leaves the two sides are about equally disposed on either side of the petiole, or of the midrib; but in *Begonia* (*e.g.*), one side is frequently much larger than the other, and the leaf is therefore oblique.

Vertical and Equitant Leaves.—In most leaves one surface is presented to the sky, the other to the earth, and if this arrangement is disturbed, the leaf will twist back again to its normal position when the restraining influence is removed. In *Iris*, however, two surfaces are apparently equally exposed, but this is not so. In that genus of plants we see through life an arrangement only seen in some other plants while in the bud—viz., they are *equitant* near the base, the whole leaf being also conduplicate. The upper portions of the leaves are in reality folded on themselves, so that what would naturally be the upper portion of the leaf is consolidated more or less in early life to the opposite half, the green portion exposed to the air being really the under surface of the leaf.

True *vertical* leaves are seen in *Callistemnon* and other Australian myrtles, and are caused by a twisting of the petiole. They, in common with the Acacias, with Phyllodia (p. 151), assist in giving a peculiar character to portions of the Australian landscape.

In *Alstrœmeria*, the leaf is twisted, so that at one time what is really the upper surface seems as if the inferior, and *vice versa*.

Leaves with no distinction of petiole and lamina are seen in the *Iris*, Daffodil (*Narcissus*) onion, leek, (*Allium porrum*[2]) and pines, and also in cedars, Arborvitæ (*Thuja* and *Libocedrus*), &c., where they are scale-shaped.

Succulent Leaves we have already seen in the stone-crop, houseleek, &c.; while *leaves as scales* are seen in the toothwort (*Lathræa*), which is parasitic on the roots of other trees, and on the vernal stem of perennial herbs "near or beneath the surface of the ground," on asparagus-shoots, &c.

The actual foliage of pines, according to Gray, originates from

---

[1] For a full account of Phyllomorphosis, see J. Rossmann's *brochure*, entitled Beiträge zur Kenntniss der Phyllomorphose, 1857.

[2] Generally believed to be a cultivated variety of *A. Ampeloprasum*, L., the largest of our British species of the genus.

a branch in the axil of their dry bud-scales, which are the primary leaves.

Leaves as tendrils (cirrhi), are seen in the pea tribe, *Fumaria capreolata*, *Methonica gloriosa*, various species of *Clematis* and *Solanum*, &c. This is, however, best seen in pinnate compound leaves. In fig. 118 is seen a leaf of the common *Lathyrus latifolius*,

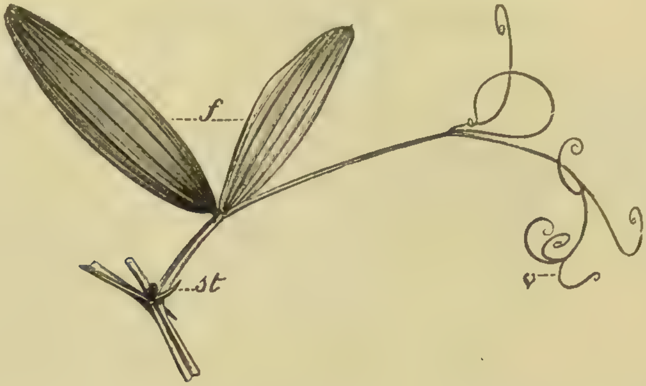


Fig. 118.—Entire leaf of *Lathyrus latifolius*, L. *st* Stipules; *f* The two leaflets remaining in a normal state; *v* Branching tendril (one-fourth nat. size).

st being the stipules, *f* the two leaflets remaining in the normal condition, *v* the branching tendril. Here it is the petiole which is prolonged upwards, with the leaflets which would have otherwise been attached to it, atrophied, and taking the form of a branching tendril. Another kind of tendril, not so easily explained, is seen in the genus *Smilax*. Here just beneath the sheathing base of the true leaf are two simple opposite tendrils. These may be explained as being (1.) either two petiolary glands which have become much enlarged and exaggerated; or (2.) the degenerated forms of two leaflets; or (3) two basilar segments of the leaf (De Candolle); or (4.) finally, as two transformed stipules. The second of these explanations, by A. St Hilaire, is the one most generally held; while the last, which we owe to the late Hugo Von Mohl, is scarcely tenable in the face of the fact that the whole of the monocotyledons (to which the *Smilaceæ*, in which is included the genus *Smilax*, belong) habitually want lateral stipules.

The last kind of leaf-tendrils we shall notice are those produced by the prolongation and union of the nerves on one side of the blade. These are seen in *Gloriosa* (*Liliaceæ*), and more particularly in *Flagellaria Indica*. We have already noticed another kind of tendrils produced by the degeneration of the branches or some other portion of the axis (p. 110). Finally, we may advert to some kinds of tendrils seen in melons (*Cucumis Melo*), *Cucurbita*, and various other plants of the order Cucurbitaceæ, the morphology of which is obscure. Here they frequently spring from under the attachment of a leaf, and have been the subject of numerous rival theories by Fabre, Clos, Naudon, Guillard, Tassi, Lestiboudois, Cauvet, Payer, Aug. St Hilaire, Stocks, and others. They may be possibly degenerated leaves, which existed at each node, stipular organs, the product of the deviation of one of the woody bundles destined for the leaf (Payer); a leaf deprived of its parenchyma, and reduced simply to its nerves (Cauvet), or an atrophied branch. Either theory has its supporters, and even the choice does not end here—for there are numerous others with[1] which the student need not, however, trouble himself. The position of a tendril is important to note, because it points out the nature of the organ. Hence in the vine the tendril is looked upon as an abortive raceme of flowers. It may be either *simple*, as in the Bryony (*Bryonia alba*), or branched, as in *Cobœa scandens* (a Mexican climbing plant cultivated in gardens.)

Leaves as Spines.—We have already considered spines as degenerations of the axis, or of some part of it (p. 110). In some other plants the nerves of some leaves alone remain, and become very indurated, the result of which is, that, as in the barberry (*Berberis vulgaris*), spines are found in the places where, under other circumstances, leaves would be situated.

Again, in the species of *Astragalus* which form the section *Tragacantha*, the common petiole of the pinnate leaf terminates in a point, and little by little, especially after the fall of the leaflets, becomes indurated, and remains attached in the form of a long spine. Lastly, in some monocotyledons we see the ribs prolonged on the surface of the leaf into a sharp spine, and not unfrequently the teeth terminate also in sharp points. Both of these modifications we see in the leaves of *Agave Americana*, which on that account is used in Algiers and elsewhere to form hedges of an almost impenetrable nature.

In the false acacia, and *Paliurus*, we find spines to the right and left of the base of the leaflets, showing that they are transformed stipules.

Pitcher-Plants.—Certain plants are popularly known by this designation on account of the leaves being either altogether or in part in the form of ascidia or hollow open sacs more or less pitcher-shaped. Something similar we have already seen in the utricles of *Utricularia*. These pitchers, which we now propose considering, are in many points, however, widely different. In *Sarracenia* ("Trumpet-flower," "Indian cups," or "Side-saddle flower,") and *Darlingtonia*, plants of the swampy regions of the north-eastern and southern portions of the Eastern United States and of California respectively, all the leaves are infundibuliform open pitchers, with a longitudinal wing on their anterior aspect. In *Darling-*

---

[1] Bull. Soc. Bot. de Fr., vols. ii. iii. iv. and xi., &c.

tonia and *S. psittacina* the "pitcher" is arched like a hood, and in the first-named genus is terminated by "a two-lobed foliaceous appendage," like the forked tail of a fish. In *Cephalotus follicularis*, a little plant of South-western Australia (fig. 119), there are two different forms of leaves. In our figure (119) is represented an entire tuft somewhat smaller than nature, and in fig. 120 is shown an example of each kind of leaves of the natural size. Round the edge of the pitcher is a sort of pad (*b*) which assists, in company with the operculum (*f'*), in closing the mouth.[1]

Fig. 119.—Entire tuft of *Cephalotus follicularis*, Labill. ; *ff* Normal flattened leaves ; *u* Ascidia, with their opercula *op* (smaller than nature).

In *Nepenthes*, a genus comprising several species found in Madagascar and the Malay Islands, there is an advance on the organisation, as seen in the foregoing plants. Here it is somewhat difficult to trace the homologues of each part of a simple leaf in the complicated structure before us. In fig. 121, one of these plants

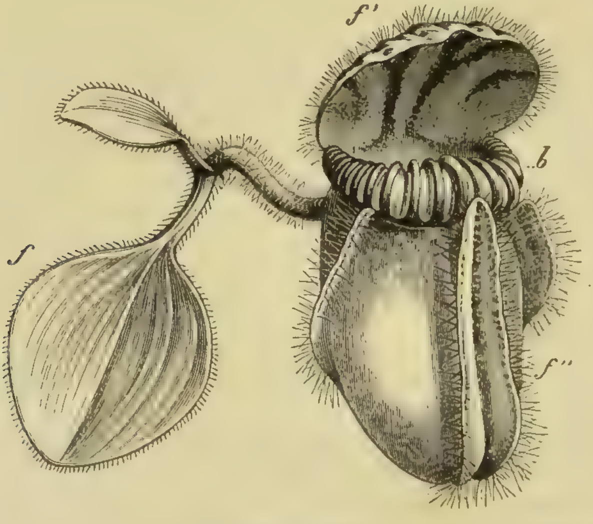


Fig. 120.—An ascidium of *Cephalotus follicularis*, isolated, and represented of the natural size, with two normal or flattened leaves, of which one, *f*, is full grown ; *f''* Body of the ascidium ; *b* Ring which guards the orifice ; *f'* Its operculum.

---

[1] Hence this is the *Calyptrimorphous* (καλύπτρα, a covering or cap, and μορφὴ, a form) mode of growth, according to the very unnecessary nomenclature of some name-manufacturer.

(*Nepenthes ampullaria*) is shown as bearing two leaves in different stages of development; (*a*) is the basilar portion, slender and

Fig. 121.—Fragment of *Nepenthes ampullaria*, Jack.

short; (*b*) a portion more expanded, thin and foliaceous, with a strong median vein; (*c*) a prolongation of that vein in the form of a slender cord; (*d e*) is the pitcher, and (*f*) the operculum. This operculum is closely applied over the orifice of the pitcher in the young state of the plant, but when it is raised the organ has then completed its development. There is no particular dilatation at the point where the cord (*c*) joins the pitcher; but on either side are two remarkable glands fringed with long hairs (*d*). In the interior of this curious organ is a glandular cellular tissue which secretes a watery liquid.

In *Heliomorpha* of British Guiana the operculum is represented by a small concave terminal appendage—the pitcher being not always completed to the summit.

Opinions are divided as to what the different portions of the organism are analogues of. Some consider that the expansion (*b*) is the true petiole, which in some leaves we have seen is developed upwards in the form of a tendril; only in this case, instead of a tendril we have a pitcher, while the lid (*f*) is looked upon as the true blade.[1] Others, on the contrary,[2] view the pitcher as the analogue of the blade, and conclude that all the inferior portions must be considered petiole and sheath. The first of these opinions has been adopted by Dr Hooker, with the modification that the tendril formed by the prolongation of the midrib carries a terminal gland, of which the pitcher is nothing more than a particular development.[3]

Finally, M. Baillon, from the study of the development of *Sarracenia purpurea*—perhaps the most common species, and the one generally cultivated in this country—considers that the origin of the lid, and of the more or less distinct lateral projections which often accompany it, is the result of an inequality in the development of the apex of the leaf, the upper margin of which increases most rapidly, and afterwards becomes slightly contracted at its base. Consequently the lid and the projections which accompany it are not a lid, but the unequal lobes of a limb that existed before them. The *keel* of the leaves of the *Sarraceniæ* appears to be nothing but an exaggeration of the nervure or projecting crest, which often stretches along the lower surface of the limb of peltate leaves from the insertion of the petiole to the bottom of the sinus presented by the base of the limb. Its vertical direction in *Sarracenia* is merely the consequence of the extreme depth acquired by the immediately peltate limb of the leaf.[4]

The pitchers which grow on the upper branches of one of the plants (at least) are said to have often adventitious rootlets developed in them,[5] which in a hot climate may be useful in supply-

---

[1] Aug. St Hilaire (Morphol. végétale, p. 142). On this view the winged margins of the petioles of *Citrus hystrix* or of Dionæa, if approximated and amalgamated, would be equivalent to the pitchers of Nepenthes, Sarracenia, &c.

[2] Duchartre, Elém de Bot., p. 310.

[3] Trans. Linn. Soc., vol. xxii., p. 415-424, pl. 69-74.

[4] Comptes rendus, Nov. 7, 1870, p. 630; and abstract in Ann. Nat Hist., vol. vii., 4th ser., 1871, p. 448.

[5] Viz., in *Dischidia Rafflesiana* (order Asclepiadaceæ), which climbs to the top of the loftiest trees—the pitchers are generally confined to its upper part. In the case of this plant they are true leaves modified, and accompanying the

ing moisture to the parched upper leaves, where there is much more evaporation than down below. Insects are often drowned in the fluid secreted in these cups, either accidentally, or are deposited there by other insects.[1] A particular species, however, has its habitat there. Some wild animals—such as monkeys—take advantage of it to quench their thirst. In most cases this water is derived from the plant itself, for the lid is so constructed that rain cannot enter. What good plants rooted in wet bogs—for such are the exact localities for *Sarracenia* and *Darlingtonia*, as the writer has observed in California—can gain from secreting or gathering water in their pitchers, it is impossible to say. Equally difficult is it to account for the presence of the dead flies, unless they act as a kind of manure. Yet *Sarracenia*, *Darlingtonia*, &c., are almost invariably crammed with insects, and the hairs which line the interior of the pitchers are so placed as to allow of the insects entering with ease, but not of escaping. In the onions (*Allum cepa*, &c.), some Convallariæ, &c., the leaves are hollow.

Bryophyllum, &c.—This genus of plants derives its name from habitually producing buds on the edges of its leaves. They are also produced as a habitual character on the edge of *Malaxis paludosa*, and on the surface of *Ornithogalum thyrsoideum*, and occasionally on the edge of *Cardamine pratensis*, *Nasturtium officinale*, and *Drosera*. In the Radick Islands of the Pacific Ocean the natives rear the *Arum esculentum* by planting the leaves. The leaves of *Gesnera*, *Gloxinia*, *Achimenes*, &c., will also produce young plants if a notch is cut in the thick veins.

PHYLLOTAXIS.[2]

That leaves are not attached to the stem and branches without regard to some fixed arrangement, is apparent on the most superficial observation. It is only, however, when we come to

---

other leaves still in their normal condition. Accordingly some have hesitated to consider these as coming under the same category as those of Nepenthes, Cephalotus, &c. Equally problematical as to their analogy are the Ascidia of the order *Marcgraviaceæ*, which open below. They are generally believed to be modified leaves of the nature of bracts. For general account of the pitcher-plants in addition to the papers quoted, see J. D. Hooker in De Candolle's Prodomus, vol. xvii.; Nature, 1871, p. 147; and notices in the same volume (p. 54, 167, and 159), by Buckton, Worthington Smith, and W. Robinson.

[1] See a most peculiar case related by Sir J. E. Smith, Introd. to Botany, chap. xvi., of a *Sphex* or *Ichneumon* dragging large flies to *Sarracenia adunca* (variolaris, W.), and forcing them under the lid. The leaves were all crammed with dead flies, and *S. purpurea* is in like manner used as a similar storehouse. His idea, that the "air evolved by these dead flies may be beneficial to vegetation," is, however, open to question.

[2] Φύλλον, leaf; ταζις, arrangement. It is also sometimes called *Botanometry*, from βοτάνη, herb, and μέτρον, measure.

examine this order more closely that we see that this arrangement is of a most complex and interesting character, involving certain mathematical principles. We have not as yet seen this in any other department of Botany. The study of this constitutes *Phyllotaxis*, or leaf-arrangement.

There are three principal ways in which leaves are arranged on the plant—viz.:

1. *Alternate* or *scattered*, when no two leaves are exactly opposite to each other, but alternate, to a greater or less extent, with the others on the same stem and branches.

2. *Opposite*, when two leaves are placed exactly on opposite sides of the same stem or branches.

3. *Verticillate*, when three or more leaves are attached around the stem at the same level. This arrangement generally occurs at nodes.

Let us consider each of these modes of arrangement somewhat more in detail.

1. Alternate Leaves.—This is the most common method of arrangement, and is normal in nearly all monocotyledons, and in many dicotyledons after the first and second nodes. It has, however, several variations, which may be briefly noticed. First, however, let us premise that all alternate or scattered leaves are disposed on the axis in a continuous spiral.

Take, for instance, a branch of the poplar, pear, prune, or peach: we see alternate leaves. But, on examining carefully, we do not find each leaf exactly above the one below; but still, following in the direction of a line drawn round the stem and touching each leaf in succession, we will find, by-and-by, one exactly over the one we commenced with. In this case it happens to be the fifth; and so, if we go winding around the stem, we will always find the same number of leaves intervening between the one with which the spiral commences and the one which is directly over it, and which, for the sake of convenience, we may call Zero. Hence, commencing with it and winding round the stem, in the leaves of the trees mentioned, we will not find one directly over it until we come to the fifth. This distance described round the stem is called the *cycle*.[1] Then commences another spiral, which ends at the tenth; over the tenth is the fifteenth, and so on. We find, further, that we had to wind *twice* round the stem before arriving at leaf 5 directly over zero, and that it has taken five leaves to complete the cycle. Let us, however, commence our description of the chief forms of Phyllotaxis in alternate leaves, by describing the simplest and then the more complicated.

Distichous,[2] or *two-ranked arrangement.*—In this variety the leaves are placed in two upright rows, each alternate leaf being

---

[1] Κύκλος, a circle.

[2] Διστιχος, in two rows.

exactly on opposite sides of the stem from the one which preceded it. Thus, the second is on the side furthest from the first; the third equally distant from the second; the fourth bears the same relation to the third, and so on throughout,—the leaves thus forming two vertical rows. Leaves arranged in this manner are known as the *distichous* or two-ranked arrangement of Phyllotaxis. Hence on one side we have the 1st, 3d, 5th, 7th, and so on; and on the other, 2d, 4th, 6th, 8th, &c., counting by a spiral line wound around the stem, and touching each leaf in succession. We find this, the simplest mode of Phyllotaxis, in all grasses and many other Monocotyledons, such as *Amaryllis*, several tropical orchids, *Aloe plicatilis*, &c., and among Dicotyledons in the linden (*Tilia*), *Paliurus*, elm (*Ulmus campestris*), camellia, &c.

Tristichous or *three-ranked arrangement.*—This we find commonly in sedges and other monocotyledonous plants, and in the elder (*A. glauca*) among other Dicotyledons. For instance, take any leaf at pleasure, and numbering it 1, pass a line round one-third of the stem as we ascend to No. 2; another third to No. 3; another brings us round to the point over No. 1, and here leaf No. 4 is placed; No. 5 is, in like manner, over No. 2, and so on. We therefore see that in this tristichous arrangement there are three vertical rows of leaves on the stems—one containing Nos. 1, 4, 7, 10, &c.; the second, 2, 5, 8, 11, &c.; and a third containing 3, 6, 9, 12,—and so on.

If a line is drawn from the insertion of one leaf to that of the next, and so on to the 3d, 4th, and the rest in succession, it will be seen that the line winds through the stem in a spiral manner as it ascends. In the first, or distichous, mode of Phyllotaxis, the second leaf is separated from the first by one-half the circumference of the stem, and having completed one turn round the stem, the third leaf begins the second turn.

Again, in the tristichous arrangement each leaf is separated by a third of the circumference or cycle, and a fourth leaf commences a second cycle, which goes on in the same way. In other words, the *angular divergence* or arc interposed between the insertion of the two successive leaves in the first (distichous) is $\frac{1}{2}$, in the second $\frac{1}{3}$ of a circle—these fractions representing not only the angles of divergence, but the whole plan of these two modes.[1] Thus the *numerator* denotes the number of times the spiral line winds around the stem before it touches a leaf directly over the one it be-

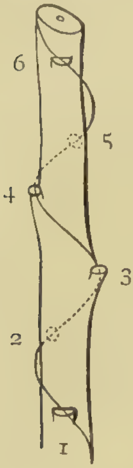
---

[1] A circle being 360°, when we state the fraction of some form of Phyllotaxis to be, say $\frac{2}{5}$, we mean to intimate that the angular divergence of each of the leaves which compose the cycle, viewed in relation to that which preceded it or followed it, is two-fifths of a circle, or 144°; when the Phyllotaxis is distichous, or $\frac{1}{2}$, the angular divergence is one-half of a circle, or 180°; when it is tristichous ($\frac{1}{3}$), it is one-third of a circle, or 120,—and so on.

gins with, while the *denominator* expresses the number of leaves that are laid down in the course which forms the cycle.

Pentastichous, quincuncial, or five-ranked arrangement (figs. 122, 123).—This is seen in the apple, peach, cherry, poplar, &c. Here we have five leaves in each cycle, the sixth commencing a second. Here we must describe two revolutions around the stem before the first leaf is exactly over the sixth, five leaves intervening, each being placed at an interval of $\frac{2}{5}$ths of the circumference. Hence $\frac{2}{5}$ is the fraction by which the arrangement is expressed—*i.e.*, 2 (the numerator) expresses the number of turns described round the stem, and 5 (the denominator) the number of leaves in the cycle, or the number of vertical ranks in such a stem. The above examples will sufficiently explain the nature of these arrangements. They do not, however, stop here, as will be seen by the following synopsis of some other forms of Phyllotaxis—each, however, proceeding on the plan as indicated above:—

Fig. 122.



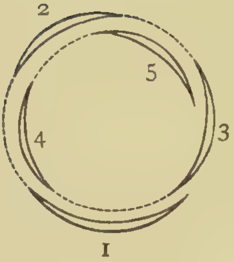


Fig. 123.

Fig. 122.—Diagram of the five-ranked arrangement of leaves. A spiral line is drawn ascending the stem, and passing through the successive scars which mark the position of the leaves from 1 to 6. It is made a dotted line where it passes on the opposite side of the stem, and the scars 2 and 5, which fall on that side, are made fainter.

Fig. 123.—A plane horizontal projection of the same; the dotted line passing from the edge of the first leaf to the second, and so on to the fifth leaf, which completes the cycle, as the sixth would come directly before, or within, the first (after Gray).

In the holly, Aconite, the tuft of leaves at the base of *Plantago*, &c., the $\frac{3}{8}$ arrangement is seen.
„ wormwood, $\frac{5}{13}$.
„ Pinus (Pinea), cones, &c., $\frac{8}{21}$.
„ *Plantago media*, &c., $\frac{13}{34}$.
„ cones of some other pines, $\frac{21}{55}$.

With a few exceptions, this consecutive series comprises within it all the variations of the kind of Phyllotaxis that are known to occur. The higher fractions chiefly occur where, as in the house-leek (fig. 127), and scales of pines, cones (fig. 126), which are modifications of leaves, the leaves are crowded on the stem, or as in the leaves of firs, &c., which are numerous and small in proportion to the circumference. Where the internodes are long and the base of the leaves broad, it is often difficult to say which leaf stands over another, or where the internodes are short, to follow the succession of the intermediate leaves, though it may be easy to follow the superposition of the leaves. However, if we can count the number of vertical rows, that gives the denominator of the sought-for fraction (*e.g.*, if 8, it is referred to the $\frac{3}{8}$ arrangement; if 13, to the $\frac{5}{13}$,—and so on). We often find the same arrangement prevailing in the parts of flowers, and a similar law regulated the Phyllotaxis of extinct plants like the *Lepidodendrons*, *Sigillarias*, &c.

We further find, on examining the series just given, that (1) *the numerator of each fraction is the sum of the numerator of the two preceding fractions*, and that *the denominator of each fraction is the sum of the denominator of the two preceding ones;* (2) we also find that *the numerator of each fraction is the denominator of the next but one preceding it.* Take, for example, the more common fractions—

$$\frac{1}{2},\ \frac{1}{3},\ \frac{2}{5},\ \frac{3}{8},\ \frac{5}{13},\ \frac{8}{21},\ \frac{13}{34}.$$

With the exception of $\frac{1}{2}$, $\frac{1}{3}$ (the *distichous* and *tristichous* arrangements), which are, in a manner, a kind of point of departure for the others, we see these curious facts exemplified. For instance, $\frac{2}{5}$ (*quincuncial* arrangement), a common fraction among leaves, is composed of the sums of the preceding numerators (1) of $\frac{1}{2}$ and $\frac{1}{3}$, and of the two preceding denominators (2 and 3) of the same fractions; in the sum $\frac{3}{8}$ which follows, it is formed by the two numerators and two denominators of the two fractions $\frac{1}{3}$ and $\frac{2}{5}$ which precede,—and so on in exactly a similar manner with the others. Again, taking $\frac{3}{8}$, we find the second rule demonstrated,—here the numerator is 3; and 3 is also the denominator of the fraction $\frac{1}{3}$, *the next but one preceding it:* so with $\frac{5}{13}$; here 5 is the numerator, the denominator of $\frac{2}{5}$, the fraction *the next but one preceding it.*

Importance of the Angle of Divergence.—N. J. C. Müller and others have shown that the angle of divergence has considerable influence on the mode in which the cell terminating the axis is divided. For instance, in the $\frac{1}{2}$ arrangement, the terminal surface of the axis is lenticular, and the cell which composes it is divided by two partitions; if the $\frac{1}{3}$ arrangement prevails, the terminal cell shows four triangular surfaces, one of which is horizontal and terminates the axis; moreover, it always remains in the same form, notwithstanding the partitions which it successively produces. Similar correlations exist among the other forms of Phyllotaxis.[1]

Secondary Spirals.—In the examples given we have seen the leaves forming but one spiral around the stem. However, in some

---

[1] Untersuchungen über das Wachsthum der einzelligen Vegationspunkte und die Bedeutung der Schimper-Braun'schen Divergenzwinkel (Verhand, der naturhistorisch-med. Vereins zu Heidelberg, vol. v. N^{r}. iii., ss. 75-77); and Bot. Zeit., 1869, 24, 25, tab. ix.; Geo. Henslow on Variations of the Angle of Divergence in *Helleborus tuberosus*, Trans. Linn. Soc., xxvi. 647.

stems, where the leaves are very numerous and closely crowded on one another, and especially when they lose their character of leaves, and are reduced to the state of scales and bracts (as in the cones of firs and the involucre of *Compositæ*), we sometimes see several parallel and oblique spirals, some towards the right, others towards the left. Take, for instance, a house-leek (fig. 127) or the cone of a fir (figs. 124, 125, 126): there is, in addition to the *primitive spiral*, which it is sometimes difficult to detect at first sight, other spirals which are called *secondary*, and which are generally much more marked than the primitive one. Again, while this primary or *generating* spiral embraces a complete series of the leaves of the stem—*i. e.*, the spiral passes through every leaf of the cluster, —the secondary spirals are invariably partial — *i. e.*, they never pass through more than a certain number of the leaves of the series.

Thus, for example, supposing each leaf numbered, the generating spiral passes through the leaves 0, 1, 2, 3, 4, 5, &c., while the secondary spirals pass through the numbers 1, 3, 5, 7, &c., or 2, 4, 6, 8, &c. It may be well, however, to remark here, that the differences between each of the numbers of the series of a secondary spiral express the number of the secondary spirals and parallels which show themselves on each side of the axis of a branch. Thus, in *Euphorbia Characias*, Richard shows that there are two secondary spirals, the one composed of the figures 1, 3, 5, 7, 9, the other of the figures 2, 4, 6, 8, 10. But the figures represented by these two spirals in union comprehend the whole series. If there are a number of secondary spirals, the figures representing each of the leaves of which each is composed present always between them a difference equal to the number of spirals.

Take, for instance, the cone of the Scotch fir (*Pinus sylvestris*). Here we see eight secondary and parallel spirals going from left to right, and comprising, when all united, the whole scales of the cone. In like manner, there are thirteen others going in an opposite direction—viz., from right to left—and, like the former, comprising all the scales in the cone. In following up one of the spirals going from left to right (or *sinistrorsal*), we see that, in commencing at scale No. 1, the spiral passes successively through Nos. 9, 17, 25, 33, but that which commences at No. 2 passes through Nos. 11, 18, 26, &c.—the difference between the numbers which form one of the secondary spirals being 8. Now this number exactly represents the number of secondary spirals—parallel and sinistrorsal. On the other hand, look at one of the secondary spirals which is directed from right to left (*dextrorsal*). Commencing at scale No. 1, that spiral passes by 1, 14, 27, 40, 33 ; or, commencing at No. 9, it passes through 22, 35, 48, 61, &c. In other words, the difference between each of the numbers in these dextrorsal secondary spirals is 13—13 being also the number of those in the cone. And so on.

Again, in fig. 124, is shown the strobilus or cone of a pine—the

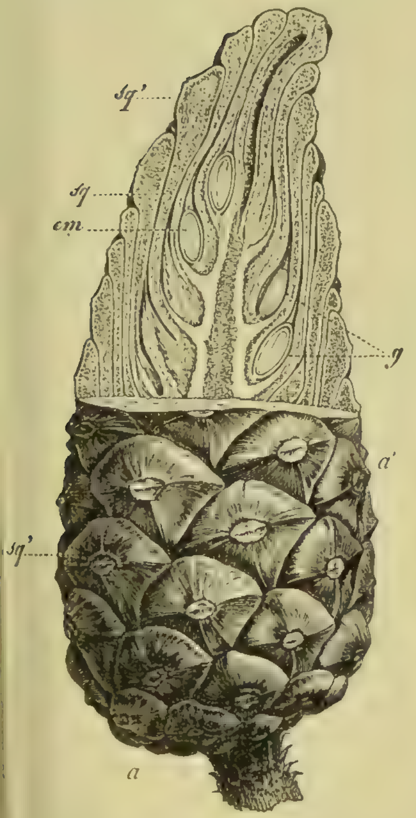


Fig. 124.—Strobilus (or cone) of a pine, with the superior portion cut away to show the central axis with the arrangement of the woody scales *sq sq'*, which cover the "naked" seeds *g*; *em* "Embryo" (or young plant) shown in longitudinal section in the seed.

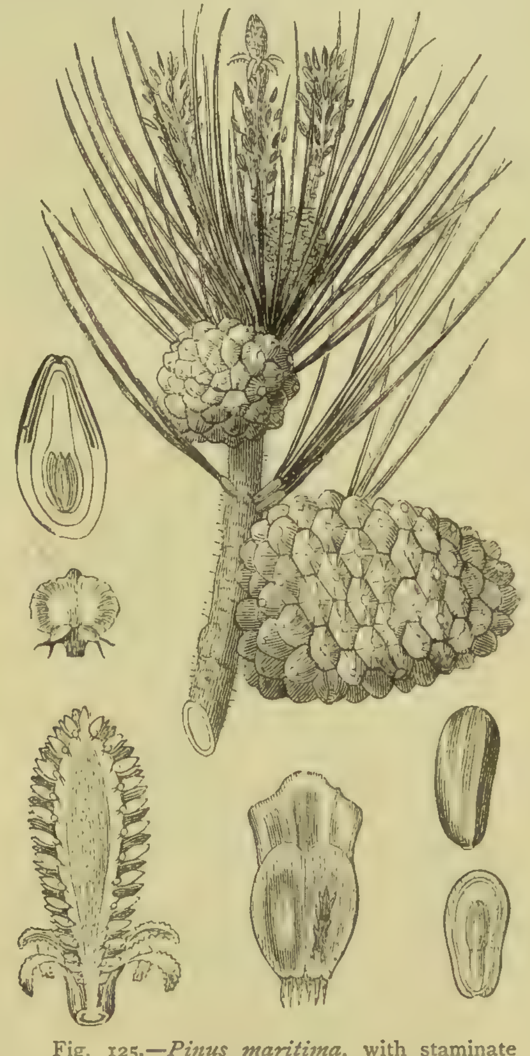


Fig. 125.—***Pinus maritima*, with staminate** flower, strobilus (cone), and various details of flowers, ovule, and seed. The leaves are in fascicles.

inferior portion, which is entire, showing distinctly the scales *sq*, with their convex quadrilateral extremities *sq'*, arranged so as to show several secondary spirals, some directly from right to left, others from left to right.

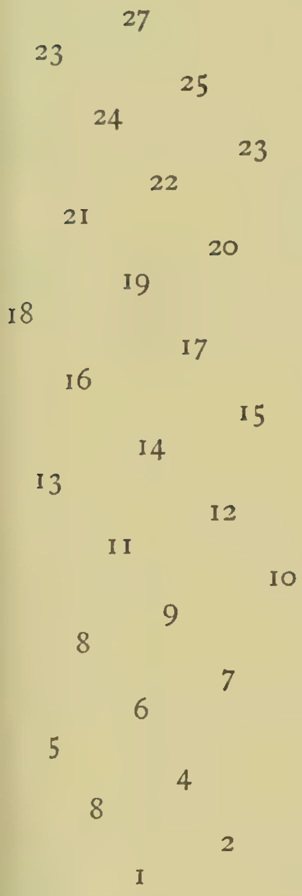
How to determine the generating spiral by the aid of the secondary spirals will have been somewhat apparent to the student from the study of the foregoing figures. However, again referring to the figures, let us explain this somewhat more in detail by their aid. The best way to do so is to write on each scale or on each leaf the number to which it is entitled, in the order of the unknown spiral—a number which the secondary spiral furnishes the means of determining. For example, if in fig. 124 there exist eight secondary spirals, apparently well marked, winding from left to right, and five going from right to left, that knowledge alone would show us how to number all the scales. It would follow that the eight parallel spirals which go from left to right, and embrace among them all the scales, would none of them have in the course of its spiral more than $\frac{1}{8}$ of the sum total. Consequently, on the spiral *a a′* (for example), if the inferior scale is numbered 1, that which would follow suit would be number 9, and the following ones successively 17, 25, 33, &c., always 8 intervening between each member. In this manner we would number all the scales of that spiral. On the other hand, the five spirals running parallel in the opposite direction—viz., from right to left—would embrace among them all the scales, and none would embrace in its spiral more than $\frac{1}{5}$th of the sum total. Accordingly, these scales would be numbered with intervals of 5 between them. Consequently, the scale which is the point of departure will be numbered 1, and those which follow suit 6, 11, 16, 21, &c. For the second of these spirals, the point of departure will be the number 9 already written, and the scales which follow it in the line of the spiral will be marked 14, 19, 24, 29, &c., since we write 9, less 5—*i.e.*, 4—beneath. For the third of these spirals, the point of departure will be the figure 17 already written, and the scales which form it will be numbered 22, 27, 32, 37, &c., above—12, 7, and 2 below. In numbering, according to the same principle, the scales which are comprised in the two last spirals directed from right to left, we will also require to inscribe a number on each. We will not, however, require in this case to do more than write the numbers in their natural sequence, 1, 2, 3, 4, 5, &c., to ascertain the course of the generating spiral, which we now see pertains to the $\frac{5}{13}$ fraction. In fact, whenever we see, as we do now, that scale 14 is directly over scale 1, the cycle is seen to be composed of 13 scales, to which belongs the number of spirals 5; hence $\frac{5}{13}$ is the fraction expressing the Phyllotaxis of the generating spiral.[1]

This will perhaps be more apparent if, following Gray, we lay down on a plane surface a vertical projection, representing the generating and secondary spirals of the white or Weymouth pine (*Pinus strobus*), alongside of the cone itself, with the scales numbered (fig. 126). The arrangement is the $\frac{5}{13}$. It might also be represented in the rosettes of leaves in the house-leek (fig. 127). Here we see a set of secondary spirals, "eight in number, with the

---

[1] Duchartre, lib. cit., p. 377.

common difference eight—viz., that of which the series 1, 9, 17, 25, is a representative. The set that answers to this on the opposite direction—viz., 1, 6, 11, 16, 21, 26, with the common difference 5—gives the numerator, and 5 + 8 the denominator, of the fraction $\frac{5}{13}$." In the figure of the cone, part of the numbers are of course out of sight on the other side of it.



Vertical projection of the $\frac{5}{13}$ arrangement.

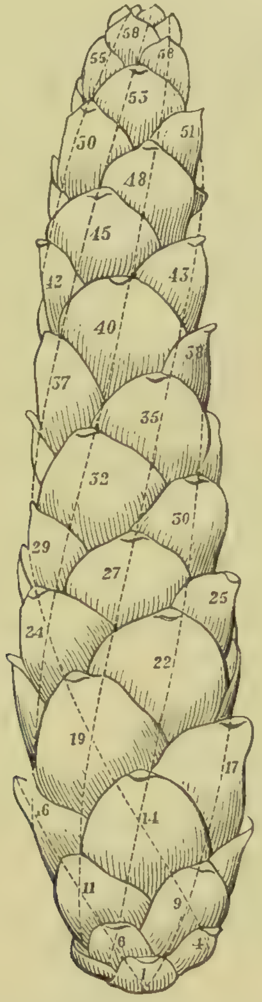


Fig. 126.—A cone of the White Pine (*Pinus strobus*) on which the numbers are laid down, and the leading higher secondary spirals are indicated; those with the common difference 8 are marked by dotted lines ascending to the right; two of the five that wind in the opposite direction are also marked with dotted lines; the set with the common difference 3 in one direction, and that with the common difference 2 in the other, are very manifest in the cone (after Gray).

Secondary spirals owe their existence to the excessive shortening of the axis bearing scales or leaves. When this axis is sufficiently long, the secondary spirals disappear, and the generating or primary one becomes apparent. In some stems of *Linum* and *Sedum* in a young state, the cylindrical leaves are much crowded, and secondary spirals are more apparent than the primary one; but as the axis lengthens, these secondary spirals disappear, and the generating one becomes apparent. So that a plant may have at its base a $\frac{2}{5}$ arrangement, and also a $\frac{3}{8}$ at its summit, as can be seen by watching the development of *Echinocactus spiralis*, one of the Cactaceæ, from the young to the adult state, &c. All dicotyledonous plants, it may also be noted, have their first leaves opposite, while later in life many of them display the alternate arrangement.

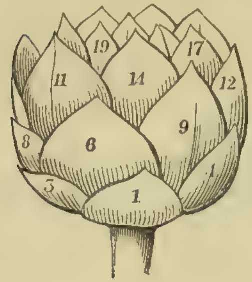


Fig. 127.—An offset of the house-leek, with the rosette of leaves unexpanded, exhibiting the $\frac{5}{13}$ arrangement, the fourteenth leaf being directly over the first leaf (after Gray).

The generating spiral may either go to the right or to the left, and may be the same in the stem and in the branches, as in the bird-cherry (*Prunus Padus*). In this case it is said to be *homodromous*.[1] If the spirals in the stem and branches turn in opposite directions (as in *Liquidambar Styraciflua*), it is, on the contrary, said to be *heterodromous*.[2] In a homodromous spiral the leaf from the axis of which the branch springs begins the spiral in that branch.

The Phyllotaxis is generally uniform in the same species, but it occasionally varies in different parts of the same plant by the multiplication by division of the ridges on which the leaves are placed, and therefore of the verticals, as in the example of *Echinocactus* just mentioned. The Phyllotaxis, however, often varies in closely allied forms. For instance, in the European larch (*Larix Europæa*) it is $\frac{8}{21}$; while in the common American larch (*L. pendula*) it is $\frac{2}{5}$; the white pine (*Pinus strobus*) is $\frac{5}{13}$; but other species of the same genus are $\frac{8}{21}$, $\frac{13}{34}$, $\frac{21}{55}$, &c.

Rectiserial and Curviserial Leaves.—In the cases of Phyllotaxis represented by the higher fractions, it is not always easy, or even possible, to say whether a particular leaf is exactly over another one—say, that the 9th, 14th, 22d, 35th, or 56th is exactly above the first, or a little to the side of it in the vertical line. In these cases the difference of the angle of divergence between a higher and a lower fraction must be very slight indeed. For instance, in the $\frac{5}{13}$ arrangement, it is 138° 24′, and in all the higher fractions it is 137°, with the addition of a variable number of minutes, which approaches nearer and nearer to 30′. MM. Bravais consider all these "mere alterations of one typical arrangement—namely, with the angle of divergence 137° 30′ 28″—which is

---

[1] Ὁμός, like, and δρόμος, course.

[2] Ἕτερος, other.

irrational to the circumference—that is, not capable of dividing it an exact number of times, and consequently never bringing any leaf precisely in a right line over any preceding leaf, but placing the leaves of what we take for vertical ranks alternately on both sides of this line, and very near to it, approaching it more and more, without ever exactly reaching it." Such forms MM. Bravais distinguish as *curviserial*, on the idea that the leaves are disposed on an infinite curve, and are "never brought into exactly straight ranks." The *rectiserial* ones are those which arrange themselves into exactly vertical ranks, owing to the leaves being arranged on an integral part of the circumference.

Other series of Cycles.—Though the forms of Phyllotaxis which we have given are those most commonly seen, yet the student ought to be aware that others—though so rarely that he need not trouble himself with more than the acquisition of a passing acquaintance with them—are met with in some plants. There are indeed two series, the terms of which are connected in this manner, that the two first terms once known, we can deduce by simple addition those which follow in the cycle of which they are component members. These two series are as follows:—

$\frac{1}{3}, \frac{1}{4}, \frac{2}{7}, \frac{3}{11}, \frac{5}{18}, \frac{8}{29}$, &c.

$\frac{1}{4}, \frac{1}{5}, \frac{2}{9}, \frac{3}{14}, \frac{5}{23}, \frac{13}{47}$, &c.

Again, in palms, Martius has shown that the spirals $\frac{1}{2}, \frac{3}{5}, \frac{5}{7}, \frac{5}{8}, \frac{8}{13}, \frac{13}{21}, \frac{21}{24}$, occur; while species of the genus *Pinus* show $\frac{2}{5}, \frac{5}{13}, \frac{5}{37}, \frac{8}{21}, \frac{21}{55}$, arrangements. These are, however, exceptional cases.

2. Opposite Leaves.—This is the next most common arrangement; and in some orders, like Labiatæ, it is the normal Phyllotaxis of all the species belonging to them. In most cases the pairs of opposite leaves alternate with one another in a *decussate* manner—that is, the second pair crosses the first at right angles, and so on: so that the third pair is directly over the first; the fourth over the second; the fifth over the third,—and so on. In these cases it will be at once evident that such leaves will describe certain vertical lines along the stem, such verticals being four, while the number of leaves is only two. Occasionally the leaves are not exactly decussate, but are arranged so that they somewhat deviate from this line, and several pairs of leaves have to be passed before we find a pair placed exactly over the pair we started with. In this case there is a spiral arrangement, coming under the head of one or other of the modes of Phyllotaxis already described. In this case, however, instead of alternate leaves we have a pair at each node.

3. Verticillate Leaves.—In this case, sometimes, the whorls are also decussate, so that the leaves of each whorl correspond to the interspaces of the leaves of the whorl beneath it. In other cases they wind spirally, so that a number of parallel spirals analogous to the secondary spirals of opposite leaves wind around the stem. In this case the angle of divergence is represented by the number of leaves which compose the vertical, and the number of spirals which are described around the stem. In this as in the case of opposite leaves, it will also be apparent that the leaves ought to form a series of marked vertical lines, of which the number is always double that of the leaves of each vertical. For instance, when there are three leaves in a whorl, there will be six vertical lines on the stem; when four, eight; and so on, just as in the case of opposite leaves there were four when the leaves were only two at each node. Verticillate leaves are said to be *ternate*, *quaternate*, *quinate*, &c., according as there may happen to be *three*, *four*, *five*, or a greater number of leaves.

Constancy or irregularity of Phyllotaxis in Genera, Species, &c. —With a few exceptions, when the opposite or alternate mode of leaf-arrangement is found in a species, it is generally always constant in every individual of that species, and often also in all the species of the family. Yet, as seen in the snapdragon (*Antirrhinum*) and myrtle, both modes may occur in the same plant. In Dicotyledons, necessarily the first leaves must be opposite, though it does not always follow that they will retain this Phyllotaxis throughout life, but may change to alternation, either in the early leaves or in those which come from the stem at a later period of life. Again, in Monocotyledons, the first leaves are necessarily alternate; but, unlike Dicotyledons, they generally retain this arrangement through life. Though we are unable to find character in Phyllotaxis constant enough to aid us in classification, yet some orders are characterised by one kind, or by the prevalence of one kind, of Phyllotaxis—*e.g.*, *Labiatæ* by decussate; *Boraginaceæ* by alternate; *Tiliaceæ* chiefly by distichous; *Cinchonaceæ* by opposite; *Galiaceæ* by verticillate, &c.

Fascicled Leaves.—The pine, larch, &c., commence with a whorl of leaves, but subsequently bear alternate ones in the form of tufts or *fascicles* (fig. 125), which are "really the leaves of an axillary bud." In this case the axis has not lengthened, otherwise the leaves would be markedly alternate, as can indeed sometimes be seen in the leaves of the larch, &c., which elongate into ordinary shoots, bearing alternate leaves. In these fascicles there may be two or more leaves, the number in a fascicle being characteristic of different species of *Pinus*. Lestiboudois, Brongniart, and other botanists, believe that the position of leaves, whether alternate or opposite, is closely connected with the arrangement of vascular bundles on the stem. When these bundles are arranged in two regular and equal groups, if the exterior bundles of each group unite, they form the midrib of the leaf, which in that case corresponds to the interval of two groups, and the leaves are *opposite.* On the other hand, they are alternate when the vascular circle of the stem has undergone a modification in its elements.

Abnormal Arrangements.—Occasionally we find some plants in which, owing either to the twisting of the stem or some abnormality in the disposition of the leaves, the foliage does not come under any of the forms of Phyllotaxis we have already described. In *Solanum Guineense*, Lamk., the leaves are arranged in twos, in a twin-like manner, side by side on the same level on one side of the stem. Numerous different explanations have been tendered regarding this by Naudin, Wydler, Clos, Cauvet, and other botanists, with a *résumé* of which we cannot, however, charge our space.[1]

Having now briefly given a sketch of the chief facts made out regarding Phyllotaxis, let us recapitulate in a few aphorisms the most salient points which we have already discussed somewhat more diffusely :—

1. Alternate leaves are disposed in a continuous spiral line.
2. In taking any leaf as the starting-point, we always find sooner or later in the line of the spiral some leaf which is exactly superimposed on it.
3. The space of the spiral line stretched between two such corresponding leaves is the *cycle.*
4. The number of leaves necessary to form a cycle is generally the same for the individuals of the same species, but often varies in the different species of the genus.
5. This spiral line may wind around the stem once, twice, or several times, before it lands at a leaf placed directly over the one it started with.
6. We express the disposition of leaves on the stem by employing a fraction, the denominator of which is formed by the number of leaves in the cycle, and the numerator by the number of turns of the spiral.
7. The more common arrangements may be represented by the following fractions :—

$$\tfrac{1}{2},\ \tfrac{1}{3},\ \tfrac{2}{5},\ \tfrac{3}{8},\ \tfrac{5}{13},\ \tfrac{8}{21},\ \tfrac{13}{34},\ \&c.$$

8. The fractions representing the composition of the various circles form a series in which each of these numbers is the sum of the numerator and denominator of the preceding fraction.
9. The *angular divergence* of leaves is the angle formed by each leaf with that which either follows or precedes it. This angle, it necessarily follows, comprises a fraction of the circumference of the stem.
10. The connection of the angle of divergence with the circumference of the circle is always expressed by the fraction which represents the circle.

---

[1] For a description of some abnormalities in the cones of *Pinus pinaster*, see Professor A. Dickson in Trans. Roy. Soc. Edin., vol. xxvi. The cones described showed transition from one spiral system to another by what has been called "convergence of secondary spirals." These transitions are due to the fusion of two consecutive scales in some one of the secondary spirals. The undisturbed set of secondary spirals, as running continuous through the two systems, Dickson terms "constants."

11. The spiral line, which touches all the leaves in its line, is the *primary* or *generating spiral.*

12. Independently of the generating spiral, there exist several others either to the right or to the left of the axis, which are very marked when the leaves are numerous and much crowded together; these are the *secondary* spirals.

13. Secondary spirals never touch a consecutive series of leaves in describing their circles around the stem.

14. Numbering each leaf, we find that the blanks in the consecutive numbers which occur in the course of a secondary spiral express the number of the secondary parallel spirals.

15. In order to ascertain the number of secondary spirals which exist in an assemblage of leaves or scales, proceed as follows: 1. Number exactly each of the scales or leaves, and ascertain thence the generating spiral, which may not be at first apparent. 2. Determine the number of leaves or scales which constitute the cycle, that number being equal to the sum of the secondary spirals which wind to the right or left of the axis. 3. Ascertain the number of turns of the spiral comprised between the two extreme points of the cycle, that number being always equal to less than the two numbers expressing the secondary spirals to the left and right. In this manner we arrive at a fraction expressing the disposition of the leaves or scales.

16. Opposite or verticillate leaves alternate generally exactly in two successive verticils. In this case they are *decussate.*

17. In some cases they are not exactly decussate, in which case the leaves describe a spiral.

18. Monocotyledons must necessarily be in their first stage alternate-leaved, and so in most cases remain through life. Dicotyledons must, on the contrary, be first opposite-leaved, but they do not always remain so in after-life.[1]

USES OF THE LEAF.

The main use of the foliage is to expose the crude juices to the action of the sun and light, and then to elaborate them for the use

---

[1] Richard, l. c., p. 127. Originally called attention to by Bonnet in 1799, *and even possibly still earlier* by Sir Thomas Browne, it is only within the last forty years, thanks to the researches of C. F. Schimper (Geiger's Magazin, vol. xxviii., and as a separate publication), Alexander Braun (Acta. Acad. Cæsar. Leop. Carol. Nat. Cur., vol. xv., 1831, and separate publication), the Brothers Bravais (Ann. des Sc. Nat., 1837 and 1839), and Alph. de Candolle, that we have attained to anything like determinate ideas on the subject. Of late years the subject has been tinkered by various inferior hands, but their observations are not of importance sufficient to occupy space by a reference to their publication, or for the author to risk the responsibility of asking the student to waste his time in perusing them in the hope of disinterring a useful fact from the insufferable quantity of pretentious verbiage in which it may be buried. An exception to this rule is, in addition to the paper of Alexander Dickson quoted, that by the same botanist on the Phyllotaxis of Lepidodendron and Knowia (Journ. Bot., 1870, p. 233), Airy's Memoir (Proc. Roy. Soc., vol. xxi.), and an Attempt to explain Phyllotaxis on the Principle of Natural Selection and the Survival of the Fittest, by Mr Chauncey Wright, originally read to the American Scientific Association, but which I only know from an abstract by Mr Bennett in 'Nature,' 1872, p. 4.

of the growing plant. To do this it absorbs air through its stomata, or in the case of water-plants through its delicate epidermis, and also discharges by evaporation, in order to thicken the crude sap which it has drawn up from the stem, a large amount of moisture. The leaf is thus at once the stomach and the lungs of the plant. Its twofold functions may therefore be better considered when we come to discuss NUTRITION as a whole in the course of the next two chapters.

DURATION, FALL, AND DEATH OF THE LEAF.

Duration.—This is variable in different species and orders of plants. In some the leaves fall soon after their development, and are called *fugaceous;* while others are called *evergreen*, from the plant on which they are found seeming as if covered with the leaves all the year round. This is, however, not so in reality, for the leaves of the last season only remain attached to the stem until the development of those of the next spring, when they fall —the result, however, being that the plant is covered with a continual mass of green leaves, which in popular belief are the same as it was clothed with in the former season. A common idea prevails that pine, and other trees of that order, do not shed their leaves. Any one who has, however, passed through a fir-wood and seen the thick carpet of the fallen acicular leaves, will be convinced that this popular notion is erroneous. The truth is, that in these trees the leaves are persistent often for several years —*e.g.*, in the "Scotch fir" (*Pinus sylvestris*) for four, while in the firs, according to the observations of Schacht, and also of Cleghorn and Brandis,[1] the leaves will often remain attached to the branches for ten or twelve years, and then fall.[2] In tropical countries plants lose their leaves during the dry season, and develop their new ones during the rainy one, as in the "Catingas" of Brazil. A similar phenomenon is seen in some plants of more temperate countries. For instance, *Anagyris fœtida*, a leguminous plant indigenous to Algeria and France, leafs in November, flowers in December, keeps its leaves during the winter and spring, finally

---

[1] Journ. of the Agri.-Hort. Soc. of India, xiv. 272 (1867).

[2] For instance, among the Himalayan Coniferæ, the leaves of *Pinus Webbiana* and *Abies Smithiana* will remain attached for 8-10 years, those of *Cedrus Deodara* 5 years, while those of *Pinus longifolia* and *P. Gerardiana* will only remain for from 2-3 years. Mr Meehan, following up the observations of Dr Alex. Dickson on the Phylloid shoots (or branches) of *Sciadopitys verticillata* (Proc. Bot. Congress, 1866, p. 124), considers that the true leaves of Coniferæ are *adnate* with the branches; that adnation is in proportion to vigour in the genus, species, or individual; and that many so-called species of Coniferæ are the same, but in various states of adnation. Since then similar views have been brought forward by Carrière.

shedding them in summer after its seeds are ripe. In *Ferula glauca, Canarina Campanula*, and *Cerinthe major*, we see much the same thing; they produce their leaves at the approach of winter, after being bare all summer. Climate has a great effect on the fall of the leaf. According to some recent observations by M. Sagot, it appears that vines and various European fruit-trees transplanted to the Canary Islands, do not there lose their leaves at the approach of winter, as in temperate countries, but they fall slowly one by one—so that the trees are rarely entirely denuded, the next year's leaves having appeared before the last season's have fallen. In most plants, however, of temperate countries, the leaves are produced in spring, last through the summer, get discoloured in autumn, and finally get stiff and lifeless, and fall at the approach of winter.[1] Such leaves are, in contradistinction to the fugacious and evergreen ones, said to be *deciduous* or *caducous*. It is a common impression that it is the action of the frost which causes the fall of the leaf. This is not so. When leaves are nipped by the frost they become black, but often remain long attached to the branches in that condition. "Death, indeed, is often more a consequence of, than a cause of, the fall of the leaf:" but leaves fall often long before the vitality has departed from the tissues of which they are composed. Again, in palms and most endogenous plants—familiarly in grasses—the leaves die, get brown and dry, but still remain attached to the stem: and in some exogenous trees even—as the beech and oak—the leaves will remain through the winter attached to the stem, though their vitality is to a great extent gone, and only fall when the new buds expand with the spring; such leaves are said to be *marcescent*. We must therefore distinguish between the *fall* and the death of the leaf.

Fall.—The apparently simple act of a leaf falling to the ground is an important physical act; but its prior detachment from the branch is not less a complicated physiological phenomenon, and has given rise to numerous rival explanations of the mechanisms involved in the process. Schacht, Mittenius, Mohl, Inman, and others, have in late years paid attention to the subject; but Mustel, Murray, Vrolik, Link, and De Candolle, have equally put forward rival theories of the mechanism of the fall of the leaf. Perhaps the explanation given by Inman is that most consonant with facts, and this we shall adopt. First, however, let us premise that the separation is caused by an *articulation* or joint, which forms between the basal end of the petiole and the stem to which it is attached. "The formation of the articulation is a vital process, a kind of disintegration of a transverse layer of cells, which cuts off

---

[1] It is rarely, however, that all the leaves on a plant last the whole summer—the lower or earlier foliage usually perishing while fresh leaves are being produced above.

the petiole by a regular line, in a perfectly uniform manner in each species, leaving a clean scar at the insertion. The solution of continuity begins in the epidermis, where a faint line marks the position of the future joint while the leaf is still young and vigorous; later the line of demarcation becomes well marked, internally as well as externally; the disintegrating process advances from without inwards, until it reaches the woody bundles: and the side next the stem, which is to form the surface of the scar, has a layer of cells condensed into what appears like a prolongation of the epidermis; so that, when the leaf separates, the tree does not suffer from the effects of an open wound. The provision for the separation being once complete, it requires little to effect it,—a desiccation of one side of the leaf-stalk, by causing an effort of torsion, will readily break through the small remains of the fibro-vascular bundles; or the increased size of the coming leaf-bud will snap them: or if these causes are not in operation, a gust of wind, a heavy shower, or even the simple weight of the lamina, will be enough to disrupt the small connection, and send the suicidal member to its grave. . . . The fall of the leaf is not an accidental occurrence, arising simply from the vicissitudes of temperature and the like, but a regular and vital process, which commences with the first formation of the organ and is completed only when it is no longer useful; and we cannot help admiring the wonderful provision that heals the wound even before it is absolutely made, and affords a covering from atmospheric changes before the part can be subjected to them."[1]

It follows, then, that in exogenous plants in which the leaf is united to the stem or branch by a moderate-sized articulation, it will fall either at the commencement of the winter, or, if it survives through that season, the enlargement of the circumference in woody plants in the spring will assuredly detach it. The same is true of leaves which fall at other seasons. In endogenous plants, however, in which there is no distinct articulation, and the base of the leaf is expanded into a sort of ochrea, as in grasses, the leaf dies, but remains attached in a dry and lifeless state.

Death.—The reason why leaves are only temporary, and of one season's duration, is as follows: The water absorbed by the root and carried up into the leaves is impregnated with a greater or less amount of mineral matter, according to the character of the soil in which the plant grows; the moisture exhaled is pure water, and accordingly the lime or other earthy matter remains behind, incrusting the walls of the vessels and cells, until, in the course of time, they are entirely choked up, and the leaf must die for want

---

[1] Inman in Henfrey's Botanical Gazette, i. 61, *teste* Gray, l. c., p. 173; and in Proc. Lit. and Phil. Soc. of Liverpool, iv. 89. See also Ledeganek in Bull. Soc. Bot. Belg., t. x. (1872).

of the necessary nourishment. Accordingly, we find that leaves in the autumn contain much more mineral matter than in the spring, and their vitality is more or less active in proportion. Thus when the leaf falls it returns to the soil a certain amount of the inorganic ingredients which the root has extracted from it in the course of the growing season.

Autumnal Colour of Leaves.—As the vessels of the petiole, &c., get closed by the inorganic deposits described, the leaf generally changes from the usual green to the various colours characteristic of the autumnal foliage of the different species. In some species —such as birches and willows—they assume a yellowish colour. In *Cissus quinquifolia* the colour is bright red. In the broad-leaved American maple (*Acer macrophyllum*) it is yellow. In the vine the colour of the autumnal leaf is also red, and the degree is in proportion to the darkness of the fruit, the black-fruited grapes having the leaves dark, while the red ones are lighter coloured; finally, in the white-fruited varieties the leaf is either yellow or feebly reddish. It is this variety of the coloration of leaves before their fall which gives a peculiar beauty to woods in the autumn—a charm even greater than they possess earlier in the year. It is probable that these changes in colour are due to changes in the chlorophyll by oxidation, though some chemists have traced them to the production of special products of a waxy nature—viz., *erythrophyll*, which is red, and *xanthophyll*, which is yellow.

Lastly, it must be mentioned that Mr H. C. Sorby has announced that he has detected in the leaves of different plants several dozen colouring matters—and far more in the petals and fruits —which number, he believes, will even be much increased by further research. Many of these colouring matters, which give the various tints to foliage, are mixed up together, so that analysis is by no means easy. He has, however, divided them into five great groups, the members of each group being related to each other not only chemically and optically, but having also a similar connection with the growth of plants. These groups are: 1. The *Chlorophyll group*, distinguished by being insoluble in water, but soluble in alcohol and bisulphide of carbon. 2. The *Xanthophyll group*, insoluble in water, but soluble in alcohol and in bisulphide of carbon, comprising two substances common in leaves— one being more and the other less yellow. 3. The *Erythrophyll group*, soluble in water, in alcohol, and in ether, and insoluble in bisulphide of carbon. Those met with in leaves are more or less purple, made bluer by alkalies, and redder by acids. 4. The *Chrysotannin group*, soluble in water, in alcohol, and in ether, but insoluble in bisulphide of carbon. This group contains a great number of yellow colours, some so pale as to be nearly colourless, and others of a fine dark golden-yellow. 5. The *Phaiophyll group*, insoluble in bisulphide of carbon, but of very variable solubility in water and alcohol. It comprises a number of more or less brown colours. The various tints of foliage depend, according to Mr Sorby, almost entirely on the relative and absolute amount of these various colours; but still much requires to be done before we are well acquainted with all these relationships. In the mean time, however, the classification of De Candolle (SECTION V.) may be received as meeting the present state of inquiry on the subject.[1]

Irregularity in Appearance of the Leaves.—In most plants the leaf appears in spring before the flowers; but to this rule we must make exception in favour of the ash, hazel, *Daphne Mezereum*, some species of *Calycanthus*, and frequently the various species of willows. In *Colchicum* and saffron the flowers develop in autumn and the leaves the spring following. On most trees the first leaves show themselves on the upper branches, but in *Stercularia platanifolia* there is an exception. In the "nettle-tree" of the south of Europe (*Celtis australis*) there is another abnormal foliation. In spring certain branches distributed irregularly on the top of the tree are covered with perfectly developed leaves and flowers, whilst upon others the buds are not even swollen by the spring sap.[2]

TERATOLOGY OF THE LEAF.

Among monstrosities to which leaves are subject may be mentioned fission or division into two or more parts, though some leaves constantly exhibit this process of fission (*Salisburia adiantifolia*, &c.) We often see this in the fronds of ferns, the tips of which bifurcate or even trifurcate. Dr Masters gives a list of about eighty species of flowering plants which have been noticed as subject to this malformation. *Phyllomania* is when there is an unwonted development of leafy tissue; *pleiophylly* is when there is an absolute increase in the number of leaves starting from one particular point, as "well as those in which the number of leaflets in a compound leaf is preternaturally increased." The leaves of *Heteracentron macrodon* have been known to produce leaflets from their upper surface, and to this monstrosity Morren has applied the term *autophyllogeny*. The four-leaved shamrock (*Trifolium repens*) is an instance of a compound leaf producing an extra number of leaflets; but five and six adventitious leaflets are almost as com-

---

[1] See Sorby, Proc. Roy. Soc., xv. 433, xxi. No. 146; Phil. Mag., xxxiv. (1867) 144; Quart. Journ. Mic. Sc., 1869, p. 43, 358; Month. Journ. Mic. Sc., iii. (1870) 229; Quart. Journ. Sc., n.s., ii. (1870) 64; Nature, 1871, p. 341.

[2] Charles Martins in Revue horticole, 1857.

mon as four, and a case is recorded in which seven leaflets were borne by the clover. Frondiferous leaves have much the appearance of branches provided with leaves, and this condition merges into that of *Gesnera*, *Cardamine*, &c., in which an adventitious bud is placed on the surface or edges of the leaves. Some Begonias form connecting links between the two conditions. In them the branchlets (ramenta) become leaf-like and bear small bulbils in the axil. Equally with the leaf the stipules are subject to a teratological increase in number. *Polyphylly* is the term applied when the members of any particular whorl are increased in number, the whorls themselves not being necessarily augmented. Leaves sometimes unite to each other by their surfaces, or even unite to the axils from which they spring. In the lime, the leaf and bract naturally unite to the peduncle. *Adventitious leaves* may form in various ways and in unusual situations. They have been seen to be produced from the hip of the rose, the ovary of the *Nymphæa*, &c.; or leaves may be produced on a usually leafless inflorescence. They may be produced in place of flower-buds, and the case of viviparous plants is one in which we see either the petiole or a part of the inflorescence so altered. *Cornute* leaves are those in which the midrib, after running for a certain distance, suddenly projects, often in a plane different from that of the leaf; then, if another part of the blade is attached to it, an interrupted leaf, as seen in some varieties of the hart's-tongue fern (*Scolopendrium vulgare*) and *Codiæum variegatum*, is produced. A cohesion of parts will sometimes produce an apparent displacement or disarrangement of the phyllotaxis. The elongation of water-leaves, to keep pace with the corresponding growth of the stem, is well seen in *Ranunculus fluitans*, &c. These and other teratological variations of the leaf lead Dr Masters to the following conclusions: " In many cases of so-called metamorphosis it is the sheath of the leaf that is represented, and not the blade. In normal anatomy the sepals, petals, carpels, and even the stamens, as a general rule, correspond to the sheath rather than to the blade of the leaf, as may be seen by the arrangement of the veins. The blade of the leaf seems to be set apart for special respiratory and absorbent offices, while the sheath is in structure, if not in office, more akin to the stem. It would not be easy, apart from their position, to distinguish between a tubular sheathing leaf and a hollow stem. The development of adventitious growths . . . is closely connected with the fibro-vascular system of the leaf, so that no sooner does a new growing part originate, than vessels are formed to connect the new growth with the general fibrous cord."[1] From this M. Casimir de Candolle is led to consider the leaf a composite structure. The morphological unit is, according to

---

[1] Teratology, p. 477.

him, the growing point and its corresponding fibro-vascular bundle.[1]

MODIFICATIONS OF THE LEAF.

These may be arranged in systematic form, chiefly as regards (1) their situation; (2) their attachment; (3) their configuration; (4) their direction; (5) the state of their surface; (6) their coloration; (7) their nervation; (8) their duration; (9) their divisions; (10) their composition; and (11) their substance.

I. Situation.

Seminal (folium seminale), when in the embryo, and then called cotyledons.

Primordial, the first leaves produced above the soil. Usually both cotyledonary and primordial leaves are only temporary, and accordingly perish soon after the ordinary leaves are developed.

Radical (radicale), leaves developed from the root. Ex. *Primrose*, *Plantago*, *Anemone Pulsatilla*, &c.; they frequently differ in shape and size from the others (fig. 117).

Cauline, *rameal* (caulinum, ramium), borne at some height on the stem or branches. Ex. *Polemonium cœruleum* (Jacob's ladder), *Paris quadrifolium* (herb Paris), &c.

Floral (florale), applied to the leaves out of the axes of which the flowers arise, and which in colour and texture do not differ from ordinary leaves. If they are different from ordinary leaves in these two respects they are called *bracts*.

II. Attachment.

Sessile (sessile), without a petiole. *Ex.* Green Alkanet (*Anchusa sempervivens*), common butterwort (*Pinguicula vulgaris*), mint (*Mentha sylvestris*), see p. 147.

Amplexicaule, or *embracing* (amplexicaule). *Ex.* Horned or sea-poppy (*Glaucium luteum*), the common poppy (*Papaver somniferum*), field gentian (*Gentiana campestris*), &c.

Semi-amplexicaul is applied when the petiole only surrounds a portion of the stem.

Perfoliate (perfoliatum), when the limb appears as if perforated (*Lonicera*) by the stem. *Ex.* Hare's-ear or thorow-wax (*Buplevrum rotundifolium*), honeysuckle, &c.

Connate (f. connata, f. coadnata), opposite leaves, united one to another by the base. *Ex.* Yellow-wort (*Chlora perfoliata*), fuller's teasel (*Dipsacus fullonum*), soapwort (*Saponaria officinalis*).

Decurrent (decurrens), when the substance of the limb prolongs itself in the form of a wing down the stem, below the point of attachment. *Ex.* Bog asphodel (*Narthecium ossifragum*), comfrey (*Symphytum officinale*), spear thistle (*Carduus lanceolatus*), &c.

Petiolate (petiolatum), furnished with a petiole. *Ex.* The majority of leaves, oaks, hawthorn, chestnut, &c.

Vaginate (vaginaris), having a sheath which surrounds the stem. *Ex.* Most grasses—*e.g.*, *Phleum alpinum* (Alpine Timothy-grass), Sea-Maram (*Psamma arenaria*).

---

[1] Théorie de la Feuille, p. 26 (*teste* Masters, l. c.)

III. Configuration.[1]

GENERAL CONTOUR.

Orbiculare (orbiculare), or *peltate* (shield-shaped), forming a circle, with the petiole inserted near the middle. Ex. *Victoria regia*, and *Brasenia peltata* (water-shield, N. O., *Cabombaceæ*). It is simply a cordate leaf with the auricles united. However, precise examples are rare (fig. 128).


Fig. 128.—Simple peltate leaf of "Indian cress" (*Tropæolum majus*, L.)

Subrotund (subrotundum), approaching to the circular form. *Ex.* Winter green (*Pyrola rotundifolia*), loosestrife (*Lysimachia repens*), round-leaved mint (*Mentha rotundifolia*), &c.

Ovate (ovatum), in the form of a flattened egg, the broadest end at the base. *Ex.* Large periwinkle (*Vinca major*). It is one of the most common forms of leaves.

Obovate (obovatum), the reverse of the above. *Ex.* Primrose, and daisy (*Bellis perennis*).

Elliptical (ellipticum), in the form of an ellipse, or without either extremity larger than the other. *Ex.* Lily of the Valley, and other *Convallariæ*, *Hieracium repens*, var.

Oblong (oblongum), three or four times as long as broad, and with a rounded extremity. The term is used with great latitude, and is often vaguely applied to contrast a not very decided form with one which is round, ovate, linear, or other precise form.

Triangular (triangulare), three prominent "angles, without reference to their measurements or direction." *Ex.* Goosefoot (*Chenopodium*), scurvy-grass (*Cochlearia Danica*), and birch (*Betula alba*).

Quadrangular (quadrangulare), with four angles. *Ex.* Tulip-tree (*Liriodendron tulipifera*).

Deltoid (deltoida), trowel-shaped, "having three angles, of which the terminal one is much further from the base than the lateral ones." *Ex.* Good King Henry (*Chenopodium Bonus Henricus*).

Rhomboid (rhombeum), rhomboid or diamond-shaped, approaching a square. Ex. *Trapa natans* (floating leaves), stinking goose-foot (*Chenopodium Vulvaria*), &c.

The four forms above named are not very constant, and are by some authors merged as varieties of some of the others named. Long use has, however, made it convenient to retain them.

Panduriform (panduriforme), fiddle-shaped, broad at the two extremities, and contracted in the middle, like a fiddle (πανδοῦρα). *Ex.* Fiddle-dock (*Rumex pulcher*).

Lanceolate (lanceolatum), narrow oblong, and tapering towards a point like a lance. *Ex.* Ribwort plantain (*Plantago lanceolata*), wild tulip (*Tulipa sylvestris*), &c.

Spathulate (spathulatum), in the form of a spatula—*i. e.*, enlarged towards the summit. *Ex.* Water-chickweed (*Montia fontana*), *Silene otites* (Spanish campion).

---

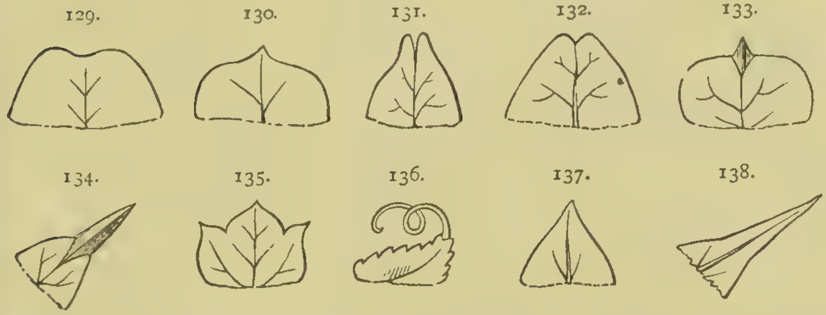
[1] As regards simple leaves.

GENERAL CONTOUR.

Linear (lineare), ribbon-shaped—*i. e.*, long, narrow, with parallel sides, and about an equal breadth throughout. *Ex.* Most grasses.

Acerose is a closely allied form. Such leaves are needle-shaped, linear, and evergreen, generally acute and rigid (firs).

Subulate (subulatum), shaped like an awl (*subula*) — *i. e.*, very straight and pointed, generally stiff. It is also only a variety of the above. *Ex.* Yews, junipers. It is sometimes applied to leaves tapering from a thickish base to a point (*e. g.*, *Salsola Kali*).



Figures showing the different forms of the apices of leaves. Fig. 129, retuse. Fig. 130, apiculate. Fig. 131, bifid. Fig. 132, emarginate. Fig. 133, mucronate. Fig. 134, cuspidate. Fig. 135, tridentate. Fig. 136, cirrhose. Fig. 137, acute. Fig. 138, acuminate.

SUMMIT.

Acute (acutum), narrowing insensibly to a point. *Ex.* Pale flax (*Linum angustifolium*), lady's slipper (*Cypripedium*), &c. (fig. 137). It is a very common form.

Acuminate (acuminatum), narrowing more or less abruptly just below the summit into a kind of sharp point. *Ex.* Common reed (*Arundo phragmites*), sea-sedge (*Scorpus maritimus*), &c. (fig. 138).

Mucronate (mucronatum), surmounted by a little point (mucro). *Ex.* Thistles, butcher's-broom (*Ruscus aculeatus*), &c. (fig. 133.)

Cuspidate (cuspidatum), surmounted by a stiff sharp spine, more distinct from the rest of the leaf than in an acuminate leaf. *Ex.* Sea-lavender (*Statice Limonum*), (fig. 134). It is, however, often used in the same sense as acuminate.

Aristate is used when the point is of a hair-like fineness.

Obtuse (obtusum), blunt, and more or less rounded at the summit. *Ex.* Primrose, snowdrop, *Hypericum quadrangulum.*

Truncated (truncatum), cut across transversely at the extremity. *Ex.* Liriodendron tulipifera.

Retuse (retusum), marked at the summit with a broad, more or less shallow sinus. *Ex.* Rumex digynus (fig. 129).

Emarginate (emarginatum), with a more or less angular notch at the summit, which is generally more acute than in the preceding cases. *Ex.* Bladder senna (*Colutea arborescens*), (fig. 132).

BASE.

Cuneate (cuneiforme, cuneatum), when broadest above the middle, with an acute tapering base, something like a wedge (*cuneus*). *Ex.* Saxifraga tridactylites.

BASE.

Flabelliform (flabelliforme), fan-shaped or broadly cuneate, and rounded at the top. *Ex.* The leaves of most Palms, Salisburia asplenifolia, &c.

Truncated, *Rounded*, &c., } with the base or apex truncated, rounded, &c. *Vide ut antea* (figs. 130, 131, 135, 136).

Cordate (cordiforme, cordatum), "heart-shaped," with the two sides of the laminæ, on either side of the petiole, rounded (forming *auricles*, or "little ears"), and with a sinus between the two, giving it somewhat the form of a heart (cor), as seen in playing-cards. *Ex.* Black bryony (*Tamus communis*).

Reniform (reniforme), "kidney-shaped," with a sinus in the middle, and forming two large lobes on either side of the petiole, the leaf broader than long. Ex. *Asarum Europæum*, *Sibthorpia Europœa*, *Oxyria reniformis*, &c.

Sagittate (sagittatum), shaped like an arrow (sagitta)—*i. e.*, prolonged at the base, with two equal, angular, acute lobes, the points of which are parallel, and with a deep triangular notch between them, in the middle of which the petiole runs. *Ex.* Water-soldier (*Sagittaria sagittifolia*), sorrel-dock (*Rumex acetosa*).

Hastate (hastatum), "halbert-shaped"—*i. e.*, prolonged at the base into two acute diverging lobes. *Ex.* Cuckoo-pint (*Arum maculatum*), Rumex Acetosella, &c.

Lunulate or *falcate* (lunulatum, falcatum), crescent-shaped, like a half-moon or a scythe, when the curved auriculæ are directed towards the stalk or from it. *Ex.* Passiflora lunata.

IV. Direction.

Erect (erectum), so placed as to approach towards the stem. Ex. *Juncus articulatus* (bulrush), Typha latifolia, Sagittaria, &c.—Or even it may be nearer, and in contact with it, when the leaf is said to be *adpressed* (adpressum). *Ex.* Zeranthemum sesamoides.

Patulate (patens, patulum), or *very patulate* (patentissimum), or horizontal, making an angle with the stem of about 45° in the first case, and at right angles in the second. *Ex.* Sea-purslane (*Atriplex portulacoides*), snap-dragon (*Antirrhinum vulgare*), of the first; while *Gentiana campestris* and *Nepeta Glechoma* (ground ivy) are good examples of the second form.

Inflexed, *incurved* (inflexum, incurvum), curved with point towards the stem. Ex. *Erica impetrifolia.*

Reflexed or *rectinate* (reflexum), with the summit curved towards the base. Ex. *Erica retorta.*—And if this is carried further, then it is *pendant* (pendulum, dependens). Ex. *Lemarus Cardiaca.*

Unilateral (f. secunda, unilateralia), all inclining on the stem towards one side. Ex. *Convallaria multiflora* (a species of Lily of the Valley).

Oblique (f. obliqua), twisted so that one part of each leaf is vertical, the other horizontal. Ex. *Fritillaria obliqua*, and some of the larger Proteæ.

Depressed (f. depressa), radical leaves, pressed close to the ground. *Ex.* Plantago major. This term is applied to stem-leaves also, but in that case is only used to express their shape, as being vertically flattened in opposition to *compressed* (various species of fig-marigold—*e. g.*, as in *Mesembryanthemum uncinatum* and *M. acinaciforme*, &c.)

V. Surface.

Plain (planum), most ordinary state. *Ex.* Portugal laurel, &c.

Crisp (crispum), irregular-plaited, like a piece of crape. Ex. *Malva crispa.* Linnæus considered this a form of disease.

Blistered (bullatum), surface marked with swollen elevations. *Ex.* Garden cabbage (*Brassica oleracea*).

Rugose (rugosum), with the veins "tighter than the surface between them," causing a series of wrinkled eminences over the surface. It is a less degree of the last. *Ex.* Various species of sage, wood-sage (*Teucrium Scorodonia*, &c.)

Undulating (undulatum), with the surface elevated and depressed in alternating lines or curves. *Ex.* Mignonette (*Reseda lutea*).

Smooth (læve), without any superficial inequalities or appendages of any description. Ex. *Euphorbia Peplus* (petty spurge), and spindle-tree (*Euonymus Europæus*).

Scabrous (scabre, asper), rough to the touch, opposed to smooth. *Ex.* Knapweed (*Centaurea nigra*), chickweed (*Stellaria Holostea*).

Verrucose (verrucosum), covered with hard or warty prominences. Ex. *Euonymus verrucosus.*

Glabrous (glabrum), deprived of hairs. *Ex.* Euphorbia Peplus, which also affords an example of "smooth" leaves.

Villose (villosum, velvetinum), velvety in feel and appearance. Ex. *Cineraria integrifolia.*

Pilose (pilosum), with long equal hairs. *Ex.* Cerastium alpinum, *Salvia pratensis* (meadow-sage).

Tomentose, cottony (tomentosum), downy, with long white, soft, silky hairs, like cotton in appearance. Ex. *Geranium rotundifolium.*

Lanose (lanatum), woolly, with long, rather firm, often reddish hairs, giving the surface the appearance of being covered with a woolly fleece. Ex. *Verbascum pulverulentum* (Hoary mullein), *V. Thapsus*, &c.

Hirsute, hispid (hirsutum, hirtum, hispidum), words expressing different degrees of the same appearance—viz., the surface covered with short, straight, stiff hairs, giving it the appearance of a brush. *Ex.* Borago officinalis (common borage).

Ciliate (ciliatum), with the margins fringed by fine hairs called *cilia*, on account of their supposed likeness to the cilia or eyelashes. *Ex.* Galium cruciatum (bed-straw).

VI. Coloration.

Coloured (coloratum), when any other colour than green. *Ex.* Arum bicolor, Amaranthus tricolor, Hedysarum pictum, Tradescantia discolor, Pulmonaria officinalis (lungwort), &c.

Variegated (variegatum), when with splatches of yellow or white on a green ground, generally the result of disease.

Discoloured (discoloratum), having the two faces coloured differently. *Ex.* Aucuba japonica (naturally green in its native country), *Mentha rotundifolia*, Elder, &c.

Spotted (maculatum), variegated with *spots* or dots, of red, blackish, or other colours. Ex. *Rhododendron punctatum*, &c.

Zonate (zonatum), marked by one or more uncertain coloured zones. Ex. *Geranium zonale.*

Glaucous (glaucum), of a glistening green colour. Ex. Holly, Portugal laurel (*Laurocerasus lusitanica*), &c.

VII. Nervation.—See in regard to this, p. 164.

VIII. Duration.—See in regard to this, p. 195.

IX. Divisions of Margin.[1]

In reference to their margin, simple leaves may be divided into two great classes—undivided and divided. Both kinds are, however (*e. g.*, the hop), frequently found on the same plant; and instances are not wanting, especially in some Californian species of oaks (*Q. agrifolia*, &c.), in which one side is serrate and the other entire. The holly is a familiar instance of a leaf the leaves of which are sometimes *divided and spinescent*, in others *entire and unarmed.* The leaf is in many respects a rather variable organ, and it is hazardous to find in its various forms a character for species without a check in characters derived from some more constant organ (*e. g.*, the flower).

Entire (*integer*, integerrimum), without any divisions. *Ex.* Orchis, lily, Daphne laureola, &c. When the margin is hard and horny it is often called *cartilaginous*, as in *Saxifraga callosa.*

Dentate (dentatum), with teeth not inclined, and rather distant. *Ex.* Atriplex rosea, cat's-ear (*Hypochœris maculata*), &c.

Serrate (serratum), with sharp teeth, directed towards the summit of the leaf, generally smaller than the preceding—"like those of a saw." *Ex.* Urtica (nettles), marsh comfrey (*Potentilla Comarum*), &c.—a very frequent state of the margin.

Crenate (crenatum), with rounded teeth or crenatures (Crenæ). *Ex.* Ground ivy (Nepeta Glechoma), golden saxifrage (*Chrysoplenium*), &c.

Bidentate, *Bi-crenate*, &c., } when the teeth or crenatures are again subdivided on their margins into serratures, crenatures, &c.

Repand or *sinuate* (repandum, sinuatum), showing a wavy outline—formed by lobes, separated one from the other by shallow depressions. Ex. *Limnanthemum nymphœoides*, *Inula dysenterica* (flea-bane).

Eroded (erosum), the border jagged or irregularly cut up, as if it had been bitten by some animal. Ex. *Senecio squalidus* (a species of groundsel). If the end is irregular in this manner it is called *prœmorse* (*Aërides*, &c.)

Incised, or cut (incisum), the margin cut by incisions, generally straight, acute, and irregular.

Laciniate[2] (laciniatum), divided in the same manner. Ex. *Syringa persica* (a species of mock-orange).

Bilobed, *Trilobed*, *Quinquelobed*, &c., } applied to express whether there are two, three, five, or other number of lobes, the Greek prefix expressing the number.

Bifid, *Trifid*, *Quadrifid*, &c., *Multifid*, } expressing whether the leaf is cut by two, three, four, or a great number of incisions.

Pinnatifid (pinnatifidum), see p. 169.

Pectinate (pectinatum), "comb-shaped," or pinnatifid, but with the lobes straight, like the teeth of a comb. *Ex.* Myriophyllum verticillatum, Hottonia palustris, &c.

Lyrate (lyratum), pinnatifid, with a large terminal odd lobe, and lateral

---

[1] See in regard to this also, p. 168.

[2] Both this and the preceding term are often used vaguely.

ones decreasing in size from the summit to the base. Ex. *Erysimum Barbarea* (a cruciferous plant of the south of Europe).

Runcinate (runcinatum), pinnatifid, with angular lobes, directed more or less to the base, like the teeth of a large saw (*runcina*). *Ex.* Dandelion.

Bipartite, *Tripartite*, &c., *Multipartite*, words to express the amount of subdivisions, two, three, or more deep divisions.

Bisected, *Trisected*, &c., *Multisected*, with the portions in two, three, or more, each *segment* being deeply divided from the others.

If the lobes are broad and diverged, the leaf is often called *palmate.*

Revolute (revolutum), when the margin is rolled backward. *Ex.* Andromeda polifolia, Tetratheca glandulosa.

Involute (involutum), the reverse of the above. *Ex.* Pinguicula.

Conduplicate (conduplicatum), when the margins are brought together. *Ex.* Roscœa purpurea. See also the terms used in PRÆFOLIATION (p. 162).

X. Composition.

The nature of *composite* leaves has been already discussed (p. 169). Their names may be briefly recapitulated in this place;—

Trifoliate, *Quadrifoliate*, *Quinquefoliate*, &c., to express whether the composite leaf is made up of three, four, five, or other number of leaflets.

Conjugate, a pinna with opposite leaflets.

Unijugate, *Bijugate*, *Trijugate*, &c., *Multijugate*, expressing whether there is one, or are two, three, or more pairs of leaflets.

Interruptedly-pinnate (interrupte-pinnatum), pinnæ with large and small leaflets intermingled.

Bigeminate (bigeminatum), with two secondary petioles, each carrying two leaflets.

Tergeminate (tergeminatum), bigeminate, and having more than two leaflets on a common petiole, at the base of two secondary petioles.

Biternate (biternatum), with three secondary petioles, each carrying three leaflets.

Triternate (triternatum), with two secondary petioles, which each carry three tertiary trileaflets.

XI. Substance.

Herbaceous, *membranous* (herbaceum, membranaceum), thin and flexible, as in the great majority of plants.

Scarious (scariosum), thin, dry, semi-transparent—*i.e.*, in the case of all leaves reduced to the condition of little scales, or in some others, like *Potamogeton crispum*; the term papery (papyraceum), when the leaf can be bent like paper, is also used, but it is unnecessary.

Coriaceous (coriaceum), hard and firm, almost like leather (corium). Ex. *Magnolia grandiflora*, *Hydrangea hortensis* (hydrangea), misletoe (*Viscum album*), &c.

Fleshy, *succulent* (carnosum, succosum, succulentum), formed for the most part of parenchyma, filled with sap. *Ex.* Sedum, Sempervivum tectorum (house-leek). These leaves often take peculiar, almost geometrical forms, and are sometimes named according to their greater or less likeness to such figures.

In the description of plants two qualifying terms are often united, either to express an intermediate state between the two, or a combination of the two. Hence we talk about a leaf being *oval-lanceolate*, *linear-lanceolate*, &c. All the terms run much into one another; so that it is often a matter of taste, rather than of precise rule, which of the combinations to select in description. There are numerous other terms commonly inserted in text-books as applied to leaves, but these have been already explained when speaking of Phyllotaxis, &c., or they are obsolete or unnecessary, and therefore a mischievous piece of over-technicalisation to perpetuate in a work of this kind. The student ought not to attempt at the commencement of his studies to burden his memory with all of these or other technical descriptive terms, but continually recur to them in the course of his studies when examining plants. Then he will understand the sense in which they are applied. He ought, however, whenever he meets with a new form of leaf, to try to obtain the correct name for it, and then to dry and preserve it for after-reference.

CHAPTER IV.

THE ULTIMATE CONSTITUENTS OF PLANTS.

THOUGH, for the sake of explaining certain facts and terms which meet the botanical student at the outset of his studies, our first chapter was devoted to the microscopic structure of plants; yet, though the cell formed the simplest *organic* element of the vegetable organism, the cell itself is composed of elements still more elementary, and we cannot go far in our studies without taking into consideration the chemical or ultimate constituents of plants. Without knowing what these are, it is impossible to rightly understand the various chemical and physiological processes which go on in the nutrition of plants, and phytological phenomena generally. Before entering upon these subjects, let us consider, so far as it is necessary for the botanical student to know, the elements which build up the whole plant—the cell as well as the more complex organs.

With this view it may be best, with Professor Johnson, to divide the substances which enter into the composition of the plant into (1) *volatile* and (2) non-*volatile* bodies, considering the latter with the composition of the ash.

THE VOLATILE PARTS OF PLANTS.

These are **Carbon**, **Oxygen**, **Hydrogen**, **Nitrogen**, **Sulphur**, and **Phosphorus**. Three of these are aeriform, the remaining three (carbon, sulphur, and phosphorus) are only volatile at a high temperature, and therefore do not usually enter into the composition of the ash. The vegetable tissue itself consists of only three of these (carbon, hydrogen, and oxygen), while nitrogen is an essential constituent of the protoplasm which plays so important a part in the formation of the cells, &c.

Carbon (C.[1]) is the chief constituent of the plant, being found on an average to form about one-half of our edible vegetables. It is shown when the substance of a piece of wood is charred in

---

[1] Chemical symbol.

the fire. Coal, which is chiefly composed of vegetable matter, contains from 40 to 80 per cent of carbon, according to its quality, its heat-giving powers depending on the percentage of this substance entering into its composition. Carbon enters the plant in the form of carbonic acid gas (CO_2), which by the action of the sunlight is decomposed, the oxygen set free, and the carbon fixed to give body to the plant.

Oxygen (O.) is also present in the plant, free or in combination. Wood, when it decays, is being oxidised—or, in other words, slowly burned, the oxygen combining with the substance of the wood in the same chemical manner as if it was burning. To designate this process Liebig has proposed the term *eremacausis*, or "slow-burning."

Nitrogen (N.), or azote, is a small but constant ingredient of plants. Boussingault showed that a seedling from which all nitrogen, except the free nitrogen of the air, is excluded, does not as it vegetates increase the amount of nitrogenised matter it originally contained, but diminishes it.[1]

Hydrogen (H.) occurs chiefly in their watery juices, but is a constant ingredient. Uniting with carbon, it forms a large number of compounds, the chief of which are the volatile oils, such as oil of turpentine, oil of lemon, &c.

Sulphur (S.) is also a constant ingredient of plants, though in small quantities. Many highly-flavoured vegetable fruits, seeds, bulbs, and roots—such as mustard, asafœtida, horse-radish, turnips, &c.—owe their peculiar flavours to volatile oils in which sulphur is an ingredient. Albumen, fibrine, and caseine, organic principles always present in the plant, also contain a small quantity of sulphur.

Phosphorus (P.) occurs in plants as phosphates of calcium, magnesium, potassium, and sodium, and may be derived from the phosphates contained in the earth. Out of these six volatile elements of vegetation are compounded, with few exceptions, all the numerous products of vegetable life; and all, with the exception of hydrogen, and sometimes nitrogen, are also found in the ash of all plants. These substances are obtained, like the non-volatile, from the aeriform and liquid food of the plant. To give a general idea of the relative proportion in which each of these elements are found in plants, we give the following composition of several dry vegetable substances (from Johnson) :—

---

[1] Comptes rendus, Nov. 28, 1853; and Ann. des Sc. Nat., ser. 4, t. i. and ii. (1854), and t. vii. (1857).

	Grain of Wheat.	Straw of Wheat.	Tubers of Potato.	Grain of Pea.	Hay of Clover
Carbon, . . .	46.1	48.9	44.0	46.5	47.4
Hydrogen, . . .	5.8	5.3	5.8	6.2	5.0
Oxygen, . . .	43.4	38.4	44.7	40.0	37.8
Nitrogen, . . .	2.3	0.4	1.5	4.2	2.1
Ash, including Sulphur and Phosphorus, .	2.4	7.0	4.0	3.1	7.7
	100.0	100.0	100.0	100.0	100.0
Sulphur, . . .	0.12	0.14	0.08	0.21	0.18
Phosphorus, . .	0.30	0.08	0.34	0.34	0.20

VEGETABLE ORGANIC COMPOUNDS OR PROXIMATE PRINCIPLES.

We now enter into a consideration of the chief organic compounds which are formed by these six elements enumerated, by the agency of the several chemical and physical forces which it is the part of the special science of chemistry to explain. These are practically unlimited, almost every plant with peculiar properties having a special principle which imparts to it that property. Hence the endless oils, acids, bitter principles, resins, colouring matters, &c., known to the chemist. Thus the active principle of tea is theine; of coffee, caffeine; of tobacco, nicotine, &c. Again, sometimes more than one essential oil is present in the plant. In the orange there are three—one in the leaves, a second in the flowers, and a third in the rind of the fruit. Yet notwithstanding, the really important principles in plants, or those which give them their properties, either useful or otherwise, are few, and may be resolved by simple, chiefly mechanical, means, into six principal groups of *proximate principles*—viz.: 1. *Water;* 2. *The cellulose group, or Amyloids*—cellulose, wood, starch, the sugars and gums; 3. *The pectose group*—the pulp and jellies of fruits and certain roots; 4. *The vegetable acids;* 5. *The fats and oils;* 6. *The albuminoid or proteine bodies.*

(1.) **Water** (H_2O) exists in all parts of the plant, but more especially in succulent or tender plants, which succulence it is the immediate cause of. It is one of the substances most essential to the life of the vegetable. It varies in different species. For instance, in a fresh specimen of mixed meadow-grass there is 72 per cent, in cabbage 90 per cent, in potato-tubers 75 per cent, in turnips 91, and in pine-wood 40 per cent. It is very abundant in succulent fruits—the strawberry and the gooseberry (*e.g.*) containing 90.23 per cent of water, the whole cherry 82.48, and the apple 84.01 per cent. Though more perceptible in fresh plants in the form of *sap*, yet even in the driest state of the plant there is a certain quantity of invisible water which can be brought out by heat. The red clover, for instance, which contains when fresh 79 per cent, when air-dried contains only 15 per cent, hay containing about a similar quantity. Dried rye and oat grain contain 14 per cent, while dried pine-wood holds 20 per cent. The water contained in the air-dried plant may be said to be *combined* water of vegetation, in contradistinction to the *free* state it is found in as expelled from the freshly-crushed plant. It is constantly fluctuating in the plant with the hygrometric condition of the air.

(2.) **The Cellulose Group, or Amyloids.**—*Cellulose* ($C_6H_{10}O_5$) is the chief component substance of cellular tissue, fibre of cotton, hemp, flax, &c.; while woody fibre is also in its first stage of a similar composition: but latterly the wood cells get filled up by *lignine*, which cannot be separated in a pure state, and has never been analysed.[1] According to Grouven and Hofmeister, lignine appears to be indigestible by herbivorous animals. The hard shells of fruits contain a basis of cellulose, which is hardened by an impregnation of lignine (p. 17). Cellulose in the air-dried state contains about 10 per cent of hygroscopic water. When put into water it swells up, and shrinks again on drying. Nitric acid in its strongest state transfers cellulose into *trinotro-cellulose*, or the explosive substance known as gun-cotton. The proportion of cellulose in various plants differs. Potato-tubers contain 1.1 per cent, wheat-grain 3.0, oat 10.3, red clover hay 34.0, oat-straw 40.0, wheat-straw 48.0 per cent.

Starch ($C_6H_{10}O_5$) is found, we have seen (p. 25), in a great variety of plants, and in some in great quantities. It is only a modification of cellulose. Trecul does not hesitate to say that vegetable membrane, composed of cellulose so called, and the starch-grains, are composed of one and the same principle in divers states of aggregation.[2] Indeed, Schroeder has traced its dissemination through the starchy layers of the fibro-vascular bundles, and its disappearance towards the point of vegetation, "at which it speedily reappears as cellulose." The potato contains

---

[1] Payen (Comptes rendus, xlviii. 324) considered that the characters of the original cellulose wall were altered by the "encrusting materials" or secondary deposits, which were, however, isomeric with that substance. Of late, however, different ideas have been broached by Frémy (Comptes rendus, t. xlviii.) This chemist recognises in the thickened cell not only cellulose, but *para-cellulose* (cells of pith, epidermis, medullary rays, &c.), *fibrose* (thickening matter of prosenchyma), and *vasculose*, the thickening matter of the vessels proper, each acting differently under the action of Schweizer's ammoniacal oxide of copper. Most chemists are, however, of Trecul's opinion (Ann. des Sc. Nat., 4e sér., x. 219), that in the present state of knowledge it is better still to hold by the old belief, and that it is neither sound nor philosophical to found new chemical substances on one character alone, and "especially on the solution of an organic matter in a liquid."

[2] Ann. des Sc. Nat., 1858, 205.

about 20 per cent, when dried 62.5 ; wheat 55.9, barley 38.5, rice (hulled) 74.1, and mustard-seed 10.8. According to Schleiden, unorganised starch (starch not in grain) exists as a jelly in several plants. Starch-grains are unacted on by cold water unless broken.

Inuline ($C_{12}H_{20}O_{10}$) closely resembles starch, and appears to replace it. It is found in the roots of the artichoke (*Helianthus tuberosus*), elecampane (*Inula Helenium*[1]), dahlia, sunflower, dandelion, chicory (*Cichorium Intybus*), and in many other compositæ. It is digested by animals, and has the same food-value as starch. In chemical percentage composition it agrees perfectly with cellulose and starch. Unlike starch, which is, unless Schleiden's view be received as correct, only found in the cells of plants in the form of very little rounded grains, inuline also exists in a liquid form in the roots above mentioned in the proportion of one part to seven of water. Iodine colours it yellow, and hence furnishes a distinctive character to recognise it by. Mohl has, however, denied that this is constant, having failed to detect it in the dahlia root (where it is abundant) by this test.[2] It is insoluble in strong alcohol. Very recently Prantl[3] has made further researches regarding this substance, his conclusions being in accordance with the former ones of Naegli and Sachs. According to this physiologist, it is a hydrate of carbon, which differs from starch, cellulose, and lichenine in never taking on an organic form, and in approaching most nearly to cane-sugar. It is found exclusively in subterranean organs (tubers, rhizomes, &c.), and "at the moment of growth is transformed into cane-sugar towards the collar of the root, then mounts into the stem in the form of starch, and thus passes towards the buds." Subsequently the starch produced in the leaves descends along the stem in the form of starch itself, or of sugar ; and it is only on its arrival in the root that it takes on the form of inuline.

Dextrine ($C_8H_{10}O_5$) has been thought to occur in small quantity dissolved in the sap of all plants ; but recent investigations show that it is not a common ingredient, having been found by Busse (according to Johnson) only in old potatoes and young wheat plants, and there in very small quantity.

The Gums are chiefly Gum-Arabic, the gum of the cherry and plum, Gum-Tragacanth, or Bassora gum, with the vegetable mucilage of various roots (mallow, comfrey) and of certain seeds (flax,

---

[1] Hence its name.

[2] Johnson (How Plants Grow, 53) says that pure inuline gives no coloration with iodine. It is possible that this may solve the seemingly contradictory statements of chemists. Mülder and Payen look upon it as a transition substance between starch and sugar.

[3] Das Inulin, 1870 ; and Bot. Zeit., 1870, No. 39.

quina, &c.) Arabine and Gum-Arabic ($C_{12}H_{22}O_{11}$) exude from the stem of various species of *Acacia*,[1] especially of Arabia and Egypt, in tear-like, transparent, and, when pure, colourless masses. When burned it leaves 3 per cent of ash, chiefly carbonate of lime and potash — the gum itself (Arabine) being chiefly a compound of lime and potash with Arabic acid. Cerasine and Metarabic acid ($C_{12}H_{20}O_{10}$) exude through the bark of the cherry, plum, apricot, and almond trees, and are "mixtures (in varying proportions) of Arabine, or the arabates of lime and potash, with *cerasine*, or the metarabates of lime and potash. Cold water dissolves the former, while the cerasine remains undissolved, but swollen to a pasty mass or jelly." Bassorine, as found in Gum-Tragacanth ($C_{12}H_{20}O_{10}$), has a great similarity to Metarabic acid in its properties. It is found on shrubs of the genus *Astragalus* (*A. creticus*, *verus*, *gummifer*, &c.), and results from a peculiar change in the walls of the cells of pith and medullary rays.[2] Vegetable mucilage ($C_{12}H_{20}O_{10}$) has nearly the same composition and characters as Bassorine, and is probably identical with it. It is an almost universal constituent of plants, particularly of the mallow order and linseed. Gum is digestible by domestic animals. The experiments of Grouven have demonstrated the fallacy of the contrary opinion.

Sucrose, *or Cane-Sugar* ($C_{12}H_{22}O_{11}$), is chiefly prepared from sugar-cane (*Saccharum officinarum*, L.), and is the ordinary sugar of commerce, though this is also got from beet-root and many other plants. It also occurs in the vernal juices of the walnut, birch, and other trees. In company with other sugar it occurs in the stems of the unripe maize, in the nectar of flowers, in parsnips, turnips, carrots, sweet potatoes, in the stems and roots of grasses, and in many fruits. On an average, there is 18 per cent in sugar-cane, 10 per cent in beet, and 2½ per cent in the sugar-maple. In wheat-flour there is also 2.33 per cent, in rice-flour 0.39, in barley-meal 3.04 per cent, and so on.

Glucose, *or Grape-Sugar* ($C_6H_{12}O_6$), occurs naturally associated with lævulose, or fruit-sugar (fructose $C_6H_{12}O_6$), in the juices of plants and in honey. It often separates from grapes in drying, and may be seen in old "candied raisins." In the sprouting of grain during the process of malting, glucose is likewise produced from starch, though it has been asserted that the sugar of malt is different, and it has been described under the name of *Maltose*. Several other sugars have been described—*e.g.*, Mannite ($C_6H_{14}O_6$), Quercite ($C_6H_{12}O_5$), Pinite ($C_6H_{12}O_5$), Mycose ($C_{12}H_{22}O_{11}$), &c. Mannite exudes from the bark of several species of ash (*Fraxinus ornis*

---

[1] E.g., *A. verra*, *A. verek*, *A. Arabica*, *A. Ehrenbergii*, &c.

[2] Mohl in Bot. Zeit., 1857.

and *F. rotundifolia*). It also exists in the sap of fruit-trees, in celery, in tangle (*Laminaria saccharina*), in edible mushrooms, in *Eucalyptus mannifera*, and sometimes is produced in viscous fermentation. *Quercite* is the sweet principle of the acorn; *Pinite* exudes from wounds in the bark of the sugar-pine of North-West America (*Pinus Lambertiana*); and Mycose is a sugar found in ergot of rye.

The various chemical properties of the sugars have proved a fertile subject of research for the chemist, but in this part of the chemistry of plant-life the botanist has little direct interest. It may, however, be noted in passing, that all this group of bodies have a remarkable facility of mutual conversion, and the result of the "machinery of the vegetable organism" is to transform them mutually into one another; so that in one stage or another of the growth of the higher order of plants we find nearly every one of them. "In germination, the starch of the seed is converted into dextrine and glucose, and so acquires solubility and passes into the embryo to feed the young plant. Here again it is solidified as cellulose, starch, or other organic principle—yielding, in fact, the chief part of the materials for the structure of the seedling." Again, the starch stored over winter in the wood of various trees, such as the maples, gets converted in spring into sugar, which rises in the sap to nourish the young buds and leaves, and so gets consolidated into cellulose, which forms the body of the plant. Mohl has shown that Gum-Tragacanth is the result of the transformation of cellulose.

(3.) **The Pectose Group** includes Pectose, Pectine, and Pectic and Metapectic acids.

Pectose (formula unknown) is supposed to occur with cellulose in the flesh of unripe fruits, and in the roots of turnips, carrots, and beets. It has never yet been separated from cellulose, and is very little known. It is supposed to constitute the bulk of the dry substance of the above-mentioned fruits and roots. Assuming that it does exist, it gives rise to the next substance—*Pectine*. Pectine ($C_{32}H_{48}O_{32}$) is produced from pectose, according to Frémy and Johnson, in a manner similar to that by which dextrine is obtained from cellulose or starch—viz., "by the action of heat, of acid, and of ferments," as in the baking of apples and pears, and in the boiling of turnips, carrots, &c., with water. In this case the starch in these fruits and roots is "slowly converted into dextrine and sugar, while the firm pectose shortly softens, becomes soluble in water, and is converted into pectine." In the ripening of fruits the same transformation takes place.

Pectosic and Pectic Acids ($C_{32}H_{46}O_{31}$ and $C_{16}H_{22}O_{15}$).—Subject to the action of a ferment (occurring in many fruits), assisted by a gentle heat, pectine is first transformed into pectosic, and afterwards into pectic acid, which two bodies compose the ordinary fruit-jellies.

Metapectic Acid ($C_8H_{14}O_9$) is produced from pectic and pectosic acid, as well as from pectine, by "too long boiling, by prolonged contact with acids or alkalies, and by decay." It is a soluble substance of sour taste, and exists, according to Frémy, in beet, molasses, and decayed fruits. Contrary to what was once supposed, Frémy[1] has shown that the pectine bodies are not convertible into sugar by the prolonged action of acids, but it is probable that in the living plant cellulose passes into pectose and pectine; and, without doubt, the reverse transformation may be readily accomplished (Johnson).

(4.) **Vegetable Acids.**—These are very numerous, nearly every order of the vegetable kingdom containing some peculiar to itself, and no class wanting them altogether. They contain more oxygen than is necessary for converting their hydrogen into water, but a smaller amount than exists in carbonic acid and water. The chief are oxalic, acetic, tartaric, malic, and citric acids.

Oxalic Acid ($C_2H_2O_4$, 2 aq.) occurs largely in the wood-sorrel (*Oxalis*), grape vine, but usually in the fruit, and in greater or less quantity in nearly all plants. The acidity of rhubarb and other vegetables is due to this acid or its salts.

Acetic Acid ($C_2H_4O_2$) occurs in plants as potassium acetate, and in other forms. It is easily produced by the destructive distillation of cellulose ($C_6H_{10}O_5 + H_2O = 3, C_2H_4O_2$).

Malic Acid ($C_4H_6O_5$) is the chief sour principle of apples, currants, gooseberries, plums, cherries, strawberries, and most common fruits, and in small quantities exists in very many plants. In combination with potash it exists abundantly in rhubarb, and as lime-salt in the nearly ripe berries of the mountain-ash (*Sorbus aucuparia*) and in berberries. As calcium malate, it occurs in some considerable quantity in the leaves of tobacco; and in the manufacture of maple-sugar often separates as "a white or grey sandy powder during the evaporation of the sap."

Tartaric Acid ($C_4H_6O_6$) occurs abundantly in the grape, from the juice of which, during fermentation, it is plentifully deposited, in combination with potash, as *argol.*

In the form of tartrates of potassium or calcium, it occurs in small quantities in tamarinds, in unripe berries of mountain-ash, in the berries of the sumach (*Rhus*, various species), in cucumbers, potatoes, pine-apples, and many other fruits.

Citric Acid ($C_6H_8O_7$) occurs in the free state in the juice of the lemon and orange, and in unripe tomatoes; in company with malic acid in the currant, gooseberry, cherry, strawberry, and raspberry; and in small quantities united to lime in tobacco-leaves, in tubers

---

[1] Annales des Chimie et de Physiques, iii. xxiv.

of the Jerusalem artichoke (*Helianthus tuberosus*, DC.), in the bulbs of onions, in beetroots, in coffee-beans, and in pine-leaves.

A curious fact about some of these acids is stated by Heyne and Zink. In various plants, such as *Sempervivum arboreum* and *Cacalia ficoides*, acids are formed during the night, which disappear during the day. In the morning the leaves of these plants are sour, tasteless at noon, and bitter at night.

(5.) **Fats and Oils** occur abundantly in the seeds of many plants. Thus the seeds of hemp, flax, beech, colza (*Brassica oleracea*), cotton, bayberry (*Laurus nobilis*), pea-nut (*Carya olivæformis*), almond, sunflower, castor-oil (*Ricinus communis*), &c., contain 10 to 70 per cent of expressible oil. An example of a solid fat of this nature is afforded by the cocoa-butter from the seeds of *Theobroma Cacoa*, that from *Cinnamomum Zeylanicum*, and by shea-butter (*Bassia Parkii*).

In some plants solid fats occur, giving a glossy coat to the leaves or forming a bloom on the fruit. According to Arendt,[1] the lower leaves of the oat-plant at the time of blossoming contain in the dry state 10 per cent of fat and wax. Scarcely any of the oils or waxes are alike in their properties, physical or chemical—and are very different from the essential oils, which are volatile. All are, however, mixtures of *stearine*, *palmatine*, and *oleine*, which are the elementary fats, and consist of carbon, oxygen, and hydrogen—the first-named element greatly predominating.

Stearine ($C_{57}H_{110}O_6$) is the most abundant of them. Palmatine ($C_{51}H_{98}O_6$) is found in great abundance in the palm-oil of Africa (*Elais Guinéensis*), and in waxberry tallow (*Stillingia sibifera*?) and other plants in India and Africa.

Oleine ($C_{57}H_{104}O_6$) is obtained from olive-oil, and occurs abundantly in the other oils. There are other elementary fats, such as Linoleine in linseed-oil, Ricinoleine in castor-oil, &c.

Some fats contain phosphorus—the seeds of the pea containing, according to Knop, "2.5 per cent of a thick brown oil, free from sulphur and nitrogen, but containing 1.25 per cent of phosphorus;" and Topler has shown that the oils of a large number of seeds contain phosphorus—*e.g.*, Lupine 0.29 per cent, Vetch 0.50, Oat 0.44, &c.

Resins, again, are found in many plants mixed with volatile oils, along with colouring matters of various kinds, the nature of which, and of other substances which we can only briefly mention, belongs to the department of the chemist and of economical botany, rather than to a treatise of this nature.

(6.) **The Albuminoid or Proteine Bodies.**—These differ from those already mentioned in containing nitrogen to the extent of 15 to 18 per cent, with a small quantity of sulphur, and in some cases

---

[1] Quoted by Johnson.

phosphorus, in addition to the ordinary carbon, oxygen, and hydrogen of the preceding five groups. The three chief albuminoids are *albumen*, *fibrine*, and *caseine*, which occur in a variety of modifications, and though in small proportions, are found in all parts of plants, being necessary for growth, but are chiefly accumulated in the seeds, especially of cereal and leguminous plants.

Vegetable albumen occurs abundantly in the clear juice of the potato-tuber, and in all plants in greater or less quantity. *Vegetable fibrine* is the chief albuminoid of wheat. "When wheat-flour is mixed with a little water to a thick dough, and this is washed and kneaded for some time in a vessel of water, the starch and albumen are mostly removed, and a yellowish tenacious mass remains, which bears the name gluten. When wheat is slowly chewed, the saliva carries off the starch and various other matters, and the gluten, mixed with bran, is left behind—so well known to country lads as "wheat-gum." Gluten, besides containing some starch and fat, is a mixture of several albuminoids.

Vegetable caseine is found in the proportion of from 20 to 27 per cent in the pea and bean, and indeed generally in the seeds of leguminous plants. The Chinese are said to prepare a vegetable cheese "by boiling peas to a pap, straining the liquor, adding gypsum until coagulation occurs, and treating the curd thus obtained in the same manner as practised with milk-cheese" (the chief ingredient of which is animal caseine)—"viz., salting, pressing, and keeping until the odour and taste of cheese are developed. It is cheaply sold in the streets of Canton under the name of *Tao-foo*." Vegetable caseine occurs in small quantities in oats, potatoes, and many plants. The caseine of leguminous plants has been designated *legumine*, and that of the oat *avenine;* while the same substance in almonds has received the name of *emulsine*. In crude wheat-gluten, two other albuminoids occur,—*Gliadine*, or vegetable glue; and *Mucidine*, which resembles gliadine, but, unlike it, does not so strongly resemble animal glue, and is less soluble in alcohol, and altogether insoluble in water.

At no time except in its dead state are albuminoids wanting in the plant, and they are especially abundant in the juices and in the seeds, when they are deposited in grains like those of starch. These grains of albuminoid matter are not in many cases pure albuminoids, but are mixed with vegetable albumen, caseine, fibrine, &c., and have been denominated *Aleurine* by Hartig, in 1855,[1] by which is meant not simply "an albuminoid, or mixture of albuminoids, but those *organised granules* found in the plant, of which the albuminoids are the chief ingredients." This substance, aleurine, appears to be very widely distributed throughout the vegetable kingdom, and to be important in nutrition. It

---

[1] Bot. Zeitung, 1855 and 1856.

is found in more or less regularly rounded grains, ordinarily colourless, but sometimes tinted brown, yellow, green, or blue, by a substance which seems to be almost superadded to it. The surface of the grains is generally foveolar, and between $0^{\text{mm.}}.00125$ and $0^{\text{mm.}}.0375$ in size. It is remarkable for the facility with which it dissolves in water, in freshly-expressed vegetable juice, and in weak acids and alkalies. It is probably owing to this fine solubility that it so long escaped the notice of observers. According to Kubel's analysis, the aleurine of the Brazilian nut gives 9.26 per cent of nitrogen, and that from yellow lupine 9.26. It is probable that, as in animals, *crystallised* albuminoids occur in plants, as first observed by Hartig.[1] Cohn has also noticed that crystalloid aleurine may be observed in the outer portion of the potato-tuber, in which it takes a cubical form, and may be best found by examining the cells that adhere to the rind of a potato that has been boiled.

Nitric acid, or rather potassium nitrate, long known to occur in vegetation, is present in most plants in very small quantities. In most mature cereals and leguminous plants it does not exceed 2 parts in 10,000 of the air-dried plant. In maize, twice this quantity is found, and in beet and potato-tops alone, of all plants examined by Frühling and Grouven, is nitric acid present to the amount of 0.025 per cent. Ammonia (NH_3) also exists in some plants, but in very infinitesimal quantities. The albuminoids vary in amount in different plants, from 1.2 per cent in green maize, fodder, and turnips, to 24.5 per cent in lentil—all through the gradation of 2 per cent in potatoes, 7.3 per cent in pea-straw, 10 per cent in the grain of barley, 13.2 per cent in wheat-grain, 22.4 in peas, and 24.1 per cent in beans.

It may be proper here to mention one or two other chemical substances of considerable scientific or economic interest, though not of fundamental chemical importance.

Chlorophyll we have already described in its botanical relations as giving the green colour to vegetation (p. 23). It is soluble in ether, and in hydrochloric and sulphuric acids, but accompanies fat or wax when they are removed from green vegetable matter by the solvent. Its composition, as found in grass, is, according to Pfaundler, carbon 60.83, hydrogen 6.39, and oxygen 32.78. It was long believed, according to the observations of Frémy,[2] that it might be separated into *Xanthophyll* (ξανθὸς, yellow, and φύλλον, leaf), a yellow colouring matter; and *Cyanophyll* (κυανος, blue, and φύλλον), a blue one,—the yellow colour of autumn leaves being probably due to the former. Micheli has of late denied the existence of cyanophyll, and experiments of Stokes go far to prove that

[1] Entwickelungsgeschichte des Pflanzenkeims, 104.

[2] Comptes rendus, 1860, 405.

it cannot be separated into the two substances cyanophyll and xanthophyll. Sachs says that in those parts of plants which are not green, but are capable of becoming so, there exists a colourless substance, *Leucophyll*, "which, in contact with oxygen, acquires a green colour, being converted into chlorophyll." Of late, N. J. C. Müller,[1] from experiments made by him, concludes that Chlorophyll in reality consists of variously-formed pigments. Contrary to the idea of M. Jodin Müller, the disengagement of carbonic acid gas (CO_2) from a solution of chlorophyll under the action of light is not sensible. So intense is its colour, that Berzelius considered that six grammes would give the beautiful green colour to a large tree; but Morol thinks this figure is exaggerated.

Glucosides are a large number of bodies which occur in plants, bitter in taste, yielding glucose or a similar sugar, and nearly allied to it. *Phloridzine*, from the bark of the apple-tree root; *Salicine*, from willow-bark; and the bitter principles of scammony, jalap, horse-chestnut, and almond,—are of this nature. Tannin is more important.

Tannin ($C_{27}H_{22}O_{17}$) is the bitter astringent principle of plants which gives certain barks their tanning powers. It is found in the bark and leaves of the poplar, oak, sumach, plum, pear, various species of coniferæ, and other trees; tea, coffee, and gall-nuts; and in small quantities in the young bean-plant, and in many buds and germinating seeds.

The researches of Schroeder[2] show that it is developed in all the cells of the bud; and when once it has made its appearance, it "persists there without appreciable change." It is constantly to be found in the youngest, and therefore most intensely vital tissues, and is probably a "sort of final product, charged with a still unknown office in the life of the cell."

The Alkaloids are numerous in poisonous and medicinal plants, and usually constitute their active principle. The most important are: *Quinine* ($C_{20}H_{24}O_2$), which along with cinchonine occurs in Peruvian bark (*Cinchona*); *Nicotine* ($C_{10}H_{14}N_2$), the principle of tobacco when it exists in combination with malic and citric acids; *Caffeine* ($C_8H_{10}N_4O_2$), in tea and coffee combined with tannic acid—in coffee it occurs to the amount of ½ per cent, but in tea sometimes is as high as 6 per cent; and *Theobromine* ($C_7H_8N_4O_2$), which resembles caffeine in character and chemical composition, and is found in the cacao-bean (*Theobroma*), from which chocolate is manufactured.

---

[1] Notiz über die Färbstoffe in Chlorophyll (Pringsheim's Jahrbuchen, 1867, Bd. vii., 1st and 2d parts, 200-208).

[2] Frühjahrsperiode des Ahorns; Pringsheim's Jahrbuch., vii. 261.

INGREDIENTS OF ASH OF PLANTS AND NON-VOLATILE INGREDIENTS.

(1.) **Non-Metallic Substances**—Oxygen, Carbon, Sulphur, Phosphorus, Silicon, Chlorine, Fluorine; (2.) **Metals**—Potassium, Sodium, Calcium, Magnesium, Iron, Manganese,—in all, 13, or if Hydrogen and Nitrogen are to be added, 15—including within this list all the elementary substances invariably present in all plants. In addition to these, however, there are occasionally present in plants—Iodine, Bromine, Titanium, Arsenic, Lithium, Rubidium, Cœsium, Barium, Aluminium, Zinc, and Copper. Several of these substances, as entering into the composition of the plant, we have already noticed. Those which are volatile by heat do not of course appear in the ash in an uncombined state. A few words on the others will suffice in this place.

Chlorine (Cl., atomic weight 35.5) is never absent from plants, and was found by Humboldt, when mixed in weak proportions with water, to facilitate the sprouting of seeds, this being probably due to the fact that when chlorine dissolved in water is exposed to sunlight, the water is decomposed, its oxygen set free, and hydrochloric acid forms. This reaction probably takes place when the germination of seeds is hastened by chlorine—the liberated oxygen being the agent which hastens the growth of the sleeping germ.—(Johnson.) Sprengel, as demonstrated by Johnson,[1] was manifestly in error when he declared that *Glaux maritima* and *Salicornia herbacea*, plants of salt marshes, exhale chlorine.

Iodine (I., at. weight 127) occurs in sea-weeds, and is found in their ashes.

Bromine (Br., at. weight 80) and *Fluorine* (F., at. weight 19) also exist in very small quantity in many plants.

Silicon (Si., at. weight 28) occurs in the form of *silica* in the stems of grasses and many other plants, and in the ashes in combination with alkalies or lime, owing to the high temperature to which it has been subjected. In the plant it occurs, however, "chiefly, if not entirely," in the free state.

Titanium (Ti., at. weight 50) and *Lithium* (Li., at. weight 7), according to Salm-Horstmar, may exist in the ashes of barley and oats.

Arsenic (As., at. weight 75) has been found, in minute quantity, in turnips which had been manured with a superphosphate, in the preparation of which sulphuric acid containing arsenic had been employed.

Potassium (K., at. weight 39) and *Sodium* (Na., at. weight 23)

---

[1] Lib. cit., p. 104.

are the only two alkaline metals invariably found in all plants, the latter being especially abundant in marine and shore vegetation.

Rubidium (Rb., at. weight 85.5) and *Cæsium* (Cs., at. weight 133), rare alkali-metals recently discovered, are probably also both present in plants. Rubidium has actually been discovered in the ashes of tobacco and beet-root; and Cœsium, though not yet detected in the ashes of plants, probably occurs there.

Calcium (Ca., at. weight 40) occurs in plants in the form of lime (Ca O., at. weight 56). In some of the Characeæ it occurs in the form of a carbonate, as also in some raphides (p. 29)—sometimes, as in the roots of some varieties of medicinal rhubarb, to the extent of from 10 to 25 per cent. It is said that the presence of similar crystals in the *Cactaceæ* causes the brittleness of plants of that order (p. 29).

Magnesium (Mg., at. weight 24) occurs in plants under the form of Magnesia (Mg O., 40).

Iron (Fe., at. weight 56), in the form of ferric oxide or hæmatite ($Fe_2O_3$160), occurs in the ashes of various plants.

Manganese (Mn., at. weight 55) occurs under the form of oxide of manganese.

Aluminium (Al., at. weight 27.4), in the form of its sesquioxide *alumina*, occurs to the extent of 20 to 50 per cent in the ashes of the clubmoss (Lycopodium); and united with tartaric—or, according to Ritthausen, malic acid—in the plant itself.

Zinc (Zn., at. weight 65.2) has been found in a variety of the yellow violet (*Viola tricolor*, var. *calaminaris*) and penny-royal (*Thlapsi alpestre*, var. *calaminaris*) growing on the refuse-heaps of the zinc-mines of Aix-la-Chapelle (Achen).

Copper (Cu., at. wt. 63.5) is found in traces in many plants, and often in the ashes of trees growing in the vicinity of manufacturing establishments, when dilute solutions containing some form of this metal may enter the soil and be absorbed by the roots. Sarzeau found it in coffee.

The Salts of Metals found in the Ash of Plants.—All the acids and oxides noticed as constituting the ashes of plants occur in the form of salts, with the exception of silica, magnesia, oxide of iron, and oxide of manganese. It is not improbable that, with the exception of silica, none of them occur in the uncombined state. These salts Professors Johnson and Church consider under the heads of—(1.) Carbonates; (2.) Sulphates; (3.) Phosphates; (4.) Chlorides; and (5.) Silicates, already mentioned. We shall follow these two distinguished chemists in their arrangement.

(1.) Carbonates. — These are potassium, sodium, and calcium. *Potassium carbonate* (K_2CO_3, 114) is found in wood-ashes after being burned, from which crude potash is obtained, which when purified yields "pearl-ash." *Sodium carbonate* (Na_2CO_3, 106), commonly called carbonate of soda, was at one time made from the ash of maritime plants (*Salsola* and *Salicornia*) in a manner similar to that by which potash is obtained from wood-ashes. It is often present in the ashes of other plants.

Calcium carbonate ($Ca\ CO_3$, 112), commonly called carbonate of lime, occurs in the ash of most plants, particularly trees. It is supposed to come mainly from the decomposition by heat of organic salts of calcium (oxalate, tartrate, malate, &c.) which exist in the juices of the vegetable, or are abundantly deposited in its tissues in the solid form. Calcium carbonate itself is, however, not an unusual component of vegetation, being found in the form of minute rhombic crystals in the cells of a multitude of plants (p. 29).

(2.) **Sulphates.**—The chief are those of potassium, sodium, and calcium. *Potassium sulphate* (K_2SO_4, 174) is obtainable from ash of wood. *Sodium sulphate* (Na_2SO_4, 142), or glauber-salt, and *calcium sulphate* ($Ca\ SO_4$, 136), are also found in the ash of most plants, especially in that of the clover, bean, and other legumes. Gypsum ($Ca\ SO_4 + 2H_2O$) is impure calcium sulphate (sulphate of lime), and may be found in microscopic crystals in the cells of many plants (bean, &c.)

(3.) **Phosphates.**—The chief are those of potassium, sodium, and calcium.

Potassium phosphates are found in the shape of the neutral and sub-phosphates to the extent of 40 to 50 per cent in the ash of the seeds of wheat, rye, maize, and other bread-grains. *Sodium phosphates.*—The chief one, found in plant-ash, is disodic phosphate ($Na_2H\ PO_4$ 12 aq.[1]) The *calcium phosphates* are many, but only two are important—viz., the *dicalcic* and the *tricalcic phosphates*, both of which, according to Johnson, "probably occur in plants." The dicalcic salt ($Ca_2H\ _2 2PO_4$, 2 aq.) probably occurs in plants, as it is stated to be an ingredient in guano. The tricalcic phosphate, or bone phosphate ($Ca_3\ 2PO_4$ or $3Ca\ O,\ P_2O_5$), constitutes 90 to 93 per cent of the ash of bones, and is also probably present in plants.

(4.) **Chlorides.**—We shall only notice those of potassium and sodium. *Potassium chloride* (KCl, 74.5) is present in the ash and juices of plants, especially of sea-weeds, in most fertile soils. *Sodium chloride* ($Na\ Cl$, 58.5), or common salt, is rarely absent from the ash of plants.

Nitrates.—In addition to the salts above described, there are present in the plant other substances which, being destructible by heat, do not appear in the analysis of the plant. We have already noticed most of them. They are *nitrates*, *oxalates*, *acetates*, *citrates*, *malates*, *tartrates*, and many less common organic salts.

Nitric Acid (HNO_3) is not unfrequently present as a nitrate in

---

[1] 12 equivalents of water (*aqua*).

the tissues of the plant, usually as nitrate of potassium or saltpetre. The leaves of the sugar-beet, sunflower, tobacco, &c., contain it. Professors Johnson and Church remark, that when such vegetables are burned the nitric acid is decomposed—often with slight deflagration, or glowing like touch-paper—and the alkali remains in the ash as carbonate.

Salts of ammonia exist in minute quantities in certain plants, but what particular ones are present is not made out; nor does their amount render the question of much importance.

In concluding this preliminary sketch of the constituents of plants, we may quote the words of the author on whose data we have chiefly relied in the foregoing remarks. In reference to the possible other combinations of substances in the plant, Mr Johnson says: "Since it is possible for each of the acids above described" (nitric, oxalic, citric, malic, tartaric, &c.) "to unite with each of the bases in one or several proportions, and since we have as many oxides and chlorides as there are metals, and even more, the question at once arises, Which of the sixty or more compounds that may thus be formed outside the plant do actually exist within it? In answer, we must remark that all of them may exist in the plant. Of these, however, but few have been proved to exist as such in the vegetable organism. As to the state in which iron and manganese occur, we know little or nothing; and we cannot often assert positively that in a given plant potassium exists as phosphate, or sulphate, or carbonate. In the ash of wheat, we judge indeed from the predominance of potash and phosphoric acid that phosphate of potassium is a large constituent of the grain; but of this we are not sure, though in the absence of evidence to the contrary we are warranted in assuming these two ingredients to be united. But calcium carbonate and sulphate have been discovered by the microscope in the cells of plants in crystals whose characters are unmistakable. For most purposes it is unnecessary to know more than that certain *elements* are present, without paying attention to their mode of combination. And yet there is a choice in the manner of representing the composition of a plant as regards its ash ingredients."

It may also be remarked that, with the exception of the volatile ingredients, the analysis of the ash gives a fair analysis of the plant, as the contents are of the kind usually present in every cell of the plant, in the cell-wall, incrusting the cellulose, and in the cell-contents.

Varying proportion of Ash.—1. The amount of ash varies in different species. For instance, red clover (whole plant dried) has only 6.7 percentage of ash, potatoes 5.1, turnips 15.5, carrots 17.1, and flax 4.3. The wood of beech has 1 per cent, grape 2.7; white birch, red pine, white fir, and larch having only 0.3 per cent. Again, the percentage in the bark varies from 1.3 in the birch to 10.4 in the cherry. In general language, ash is abundant in succulent foliage, and small in seeds, wood, and bark.

2. It also varies in different parts of the same plant. The wheat-grain contains 2 per cent, while the straw yields 5.4 per cent. In sugar-beet tops the ash is 7.5, and in the roots 4.4 per cent; and in the ripe oat, Arendt found that the amount of ash varied from 2.6 per cent in the ear to 10.5 per cent in the two upper leaves.

3. In general, the *upper* and *outer* parts of the plant contain most mineral matters. Norton[1] found that the top of the oat-leaf gave 16.22 per cent of ash, while the bottom yielded but 13.66 per cent. Wood, seed, and the lower and inner part of the plant are poorest in ash. The stems of herbaceous plants come next in richness, while the leaves of herbaceous plants are the richest of all.[2]

4. The same plant at different periods of its growth varies in the proportion of ash, in dry matter yielded both by the whole plant or particular portions of it. Thus Norton found that on the 4th of June the leaves of the oat had 10.8 per cent of ash, the stem 10.4. On the 23d July the leaves had 16.4, the stem 7.9, the nodes 10.9, the chaff 9.1, and the unhusked grain 3.6 per cent of ash. Finally, on the 3d September the leaves had 20.9, the stem 8.3, the nodes 10.7, the chaff 27.4, and the unhusked grain 3.6 per cent of ash. In fact, there was a constant increase in the ash of the leaves and chaff as the plant grew older, the nodes keeping pretty uniform in their ash; the stem constantly decreased in ash as it grew older, except at the period of ripening, when it increased; while the unhusked grain "at first suffered a diminution, then an increase, and lastly a decrease again." Similar observations, though with different results, have been made by Pierre on the colza (*Brassica oleracea*), by Bretschneider on the sugar-beet, by Wolff on the potato, and by Anderson on the potato. The general result was, *that the proportion of ash of the entire plant diminished regularly as the plant grew old.*

5. The nature of the soil—loamy, silicious, argillaceous—influences the percentage of ash.

6. Different varieties of the same species take up different quantities of volatile matter, and accordingly show differences in their ash proportion. The "Fortyfold" potato was shown by Herepath to yield only 3.9 per cent of ash, while "White's apple" yielded 4.8, and "Prince's Beauty" 3.6.

7. Different *individuals* of the same *species* show different percentages of ash, even though growing side by side—showing that each plant may have different nutritive powers, just as different individuals of the same animal have. For instance, Pierre found in extremely feeble plants of colza only 8 per cent of ash, while

---

[1] Silliman's Journal, 1847.

[2] Johnson, l. c., p. 126.

extremely strong plants gave 14.3 per cent, probably to be accounted for by the greater quantity of leaves on them. The varying proportion of ash is also due to the varying effects of soil, light, shade, and other circumstances, increasing or decreasing the different parts of the plant, which we have seen vary in composition. *Of all the parts, the seeds are least liable to vary in composition, so far as the ash is concerned.* Wolff has given the following general averages of ash :—

Annual and Biennial Plants.		Perennial Plants.	
Seeds,	3 per cent.	Seeds,	3 per cent.
Stems,	5 ,,	Wood,	1 ,,
Roots,	4 ,,	Bark,	7 ,,
Leaves,	15 ,,	Leaves,	10 ,,

In general, it may be concluded from the above facts that three propositions are proved—viz. :

(1.) Ash ingredients are indispensable to the life of the plant, as analysis never fails to recognise, even in the lowliest species, a proportion of fixed ingredients; and it has been found from numerous experiments that no plant can grow in the absence of those substances found in the ash.

(2.) Ash percentages have a limited range of variation, never falling below or exceeding certain limits.

(3.) "Each part or organ (cell) of the plant contains a certain, nearly invariable, amount of fixed matters, which is indispensable to the vegetative functions. Each part or organ may contain, besides, a variable and unessential or accidental quantity of the same." That every part of the ash is not equally important may also be believed; but what is most and what least important, is a question as yet *sub judice.*

Professors Johnson and Church have given an extensive table of the chemical composition of the various agricultural plants, from which they have deduced the following general conclusions :—

1. The ash of agricultural plants invariably contains ten ingredients, and these ten ingredients are found in nearly all parts of them. They are as follows :—

Basic constituents.	Acid constituents.
Potash, K_2O.	Chlorine, Cl.
Soda, Na_2O.	Sulphuric trioxide, SO_3.
Lime, $Ca O$.	Phosphoric pentoxide, P_2O_5.
Magnesia, $Mg O$.	Silicic dioxide, $Si O_2$.
Ferric oxide, F_2O_3.	Carbonic dioxide, CO_2.

We have already discussed these.

2. Normal specimens of the same plant do not differ much in ash percentage.

3. Different parts of the same plant usually exhibit decided differences in the composition of their ash.

4. Similar plants, and especially the same parts of the same plant, exhibit a close agreement in the composition of their ashes; while plants which are unlike in their botanical characters, are also unlike in the proportions of their fixed ingredients.

5. The ash of the same species of plant is more or less variable in composition, according to circumstances. The causes inducing this variation are—(α) the stage of growth of the plant; (β) the vigour of its development; (γ) the variety of the plant, or the relative development of its parts; (δ) the soil or the supplies of food, both natural and artificial; (ϵ) the season and climate.

6. To pronounce on the normal composition of the ash of a plant is a matter of much difficulty and uncertainty, and can only be given from an average of many analyses.

Uses of the Mineral Ingredients of Plants.—At one time it was supposed that the substances found in the ashes of plants were unessential to their growth. The progress of chemical analysis has long ago dissipated this idea, as well as the still more erroneous one that they were the products of growth. No doubt Mülder considered that he could detect no ash ingredients in some fungi, such as *Mycoderma vini*, nor in the moulds produced in milk-sugar. Still these exceptional cases found in plants like fungi, the nature of which is in many things exceptional to the general character of vegetable life, do not materially affect the general rule. To ascertain what ingredients are essential, and what less so, numerous experiments have been instituted by different chemists and agriculturists—notably, Prince Salm-Horstmar, Sachs, W. Knop, Stohmann, Nobbe, Siegert, Wolff, Lawes and Gilbert, and others. Most of them commenced these experiments by growing plants in certain solutions, and watching the results—as to what substances were first and chiefly abstracted, and so on. No doubt water-culture does not supply all the conditions of growth, the soil independently of its mere chemical constitution having certain mechanical influences which are not without their effects on the result; yet from the facility it affords to watch the whole process of growth, and to vary the conditions of life, it has proved of great importance to vegetable physiology, and seems destined to still further increase our knowledge. The result of these experiments, as far as they have hitherto gone, is, that six out of the ten ash ingredients — viz., *Potash*, *Lime*, *Magnesia*, *Phosphoric Protoxide*, and *Sulphuric Trioxide*—are absolutely necessary to the life of agricultural plants at least. These we have already considered. Let us now briefly say a few words on some other more dubiously essential constituents of plants.

Soda and Potash.—It has been doubted whether sodium is absolutely necessary to the life of plants, having been found by some analyses entirely wanting in some agricultural species; but this seems scarcely well established, though so late as 1869 Peligot denied its necessity in the nutrition of plants, soda, according to him, being equally absent in potatoes grown close to or at a distance from the sea. The amount of sodium varies greatly. Salm-Horstmar, as the result of his investigations, considered that "in the early vegetative stages of growth, soda, while advantageous, is not essential, but that for the perfection of fruit an appreciable though minute quantity of this substance is indispensable." Stohmann's experiments led to a similar conclusion; but on the other hand, Knop, Nobbe, and Siegert, after experiments with maize and buckwheat, came to contrary conclusions. The general results may be summed up in Johnson's words: (1) That soda is never *totally* absent from plants; but that (2), if indispensable, only a minute amount of it is requisite. (3), That the foliage and succulent portions of the plant may include a considerable amount of soda that is not necessary to the plant—that is, in other words, *accidental*. All animals require *soda;* and hence the food of animals being derived indirectly at least from the vegetable kingdom, "it is a wise provision that soda is *contained* in, even if it is not indispensable to plants." Sodium cannot wholly replace potash in plants, as proved by the experiments of Salm-Horstmar, Knop, and Schreber, though Cameron shows that this can be partially the case. Cultivated plants contain less sodium and more potassium than the wild—even sometimes, as in the case of wild and cultivated asparagus, to the extent of 18.8 per cent of potash in the wild and 50.5 per cent in the cultivated, and 16.2 per cent of soda in the wild and a mere trace in the cultivated plant.

These conclusions, that soda can only partially replace potash, cannot be received in the case of strand plants. Asparagus, beet, and carrot, though grown close to the shore, where they must receive much soda compounds, are perfectly capable of growing inland in soils where these must be almost entirely absent. On the other hand, *Salsola* and Samphire (*Crithmum maritimum*) never stray inland, and soda is never absent from these forms of vegetation. Cadet found that the seeds of *Salsola kali* (prickly saltwort) "sown in common garden-soil, gave a plant which contained both soda and potash" (as do the ordinary plants of *Salsola tracheata* and *Salicornia herbacea* (glasswort), analysed by Göbel from the Caspian steppes): "from the seeds of this, sown also in garden-soil, grew plants in which only potash salts, with traces of soda, could be found." Professor Dickie of Aberdeen found that in *Armeria maritima* (sea-pink), *Cochlearia officinalis* (scurvy-grass) and *Plantago maritima* (sea rib-grass), the soda which is found in these, when growing by the sea-shore, is on the mountains replaced to a great extent by potash, and the iodine altogether disappears

In "Halophytes"[1]—such as various species of *Salsola*, *Salicornia*, *Halimocnemum*, &c.—soda is found in such abundance as to render them valuable in commerce as sources of supply for that substance.

Though sea-water only contains potash to the amount of $\frac{1}{30}$ of the soda, yet algæ, which derive their nourishment exclusively from the sea, contain in general as much potash as soda, if not more.[2]

Iron (Fe.)—A minute quantity of ferric oxide (Fe_2O_3) is absolutely essential to growth, even though this requires sensitive tests to detect. Maize refuses to grow in the entire absence of it, but flourishes if its roots are simply bathed for the first four weeks in a solution in which a piece of ferric oxide (which is very insoluble) is suspended. In the wood, and especially in the bark of trees, oxide of iron (ferric oxide) has been found to the extent of from 5 to 10 per cent. In aquatic plants there is a large percentage. In the ordinary duck-weed (*Lemna trisulca*), Liebig found 7.4 per cent. In the ash of the leaves of *Trapa natans*, Gorup-Besanez found 29.6 per cent, and in the pericarp of the same plant 68.6 per cent. An even more direct function of iron is that it is essential to the development of chlorophyll. If iron is withheld, the plant may send out pale shoots at the expense of the rest of its structure ; but these will not really increase in size and weight, and will not even, in the presence of sunlight, attain a green colour. When we know that the power of the leaf to decompose carbonic acid and assimilate carbon is dependent on chlorophyll, we can readily understand how in its absence there can be "no proper growth, no increase at the expense of the external atmospheric food of vegetation." Manganese cannot take the place of iron in the office described.[3]

Oxide of Manganese (Mn_3O_4) is perhaps unessential to the life of the plant. It generally accompanies iron. In the ash of *Trapa natans*, above alluded to, there was found from 7.5 to 14.7 per cent. It sometimes exists in even greater quantity than the iron—*e.g.*, in the leaves of the beech (*Fagus sylvatica*) Fresenius found 11.2 per cent of oxide of manganese and only 1 per cent of iron ; and Neubauer, in the ash of oak-leaves (*Quercus robur*), 6.6 of the former and 1.2 per cent of the latter. Still, as already remarked, it is a question whether it is absolutely needful for all plants—Salm-Horstmar taking the lead in the affirmative ; while Sachs, Knop, Birner, Lucanus, and others, are inclined to take the contrary view. Most probably the latter view is the correct one.

---

[1] ἅλς, salt ; φύτον, a plant.

[2] Forchammer in Journal für Prakt. Chem., s. 36 ; Anderson, Trans. Highland and Agric. Soc., 1855-57, p. 349.

[3] Risse in Sachs' Experimentale Physiologie (French trans.), p. 143.

Chlorine (Cl.)—The probabilities are that it is present in all plants, and is essential to their growth. In nature it is usually associated with sodium in the form of common salt: and in this form they most likely both enter the plant, for when the one is present in large quantity, the other exists in corresponding quantity. In wheat the average amount of chlorine is only 0.08 per cent. In the stems of plants which grow in soils containing much common salt, such as strand and marine plants, chlorine is very abundant. Still there is a doubt as to whether it is absolutely indispensable to the life of the plant,—Salm-Horstmar, Leydhecker, Birner, Lucanus, Nobbe, and Siegert thinking that a minute trace is essential; while Knop takes a contrary view, as the result of his experiments with the maize plant. As far as agricultural plants are concerned, it is probable that chlorine, if indispensable, *is* essential to plants only in minute quantity—buckwheat, vetches, and perhaps peas, requiring a greater quantity, and the foliage and succulent parts of a plant containing a considerable quantity, which may, however, be "not indispensable to the life of the plant."

Strand plants require chlorine, but whether united to potassium or sodium is immaterial. Regarding the functions of chlorine, Johnson remarks that both Nobbe and Leydhecker found that buckwheat grew quite well up to the time of blossoming without chlorine; and that the use of it, according to these experimentalists, is to assist in transferring the starch-granules which are organised in the mature leaves to the newer organs, and especially to the fruit. In the absence of chlorine, the terminal leaves of buckwheat became thick and fleshy, from extraordinary development of cellular tissue; "at the same time they curled together, and finally fell off upon slight disturbance. The stem became knotty, transpiration of water was suppressed, the blossoms withered without fructification, and the plant prematurely died. The fleshy leaves were full of starch-grains; and it appeared that, in the absence of chlorine, the transfer of starch from the foliage to the flower and fruit was rendered impossible."

Silica (SiO_2) is a variable element of plants, and is "always present in the ash of agricultural plants when they grow in natural soils." In wood-ash it ranges from 1 to 3 per cent, often 10 to 20, or even in the pine up to 30 per cent. Turnip-leaves contain 3 to 10 per cent, oat 11 to 58 per cent (especially in the stem), lettuce 20 per cent, oak-leaves 31 per cent, and beech-leaves 26 per cent. The cuticle of many plants contains a great amount of silica—this giving the stability of stem to many herbaceous plants, and the hardness of wood to arboreal species. The Cauto tree of South America (*Hirtella silica*) has the texture of soft sandstone, and speedily blunts the woodman's axe; and in Trinidad the natives mix its ashes with clay to make pottery. The bark yields 34 per cent of ash, of which 96 per cent is silica.[1] The ash of the well-known bamboo contains 70 per cent of silica, and the joints of the stem often contain concretions known as *Tabasheer*, which Russel and Smithson (Macie, the founder of the Smithsonian Institution) discovered to be a hydrated silica.[2] The ash of the common "Dutch" or "scouring rushes" (so called because in Holland they are used to polish brasses) contains 97.5 per cent of silica. The *actual* amount of silica in the different British species of *Equisetum* varies from 6.30 per cent in *Equisetum arvense*, to 23.61 per cent in *Equisetum Telmateia*. The ash of the straw of most of the cereals and grasses contains silica to the amount of from 40 to 70 per cent. Hence burnt straw is used to give a last polish to marble. After a hay-stack has been burned down, frequently little stony masses may be found among the ashes. These are composed of melted silicates. In the *Characeæ* there is a curious variability of the substance which gives the hard incrustation to their thread-like leaves. In *Chara translucens* it is silicic acid, in *C. vulgaris* silicic acid and carbonate of lime, and in *Chara hispida* carbonate of lime solely. In the *Carices* and *Juncaceæ* there is also much of this substance. In all these plants the cuticle is richest in silica. It has also been found by Wottstein that the oldest parts of plants contain most silica. In the ash of the wood of a "Scotch fir" (*Pinus sylvestris*) 220 years old there was found 32.5 per cent, and in one 135 years old only 15.1. In the bark of the same tree, at the two ages given, the amount of silica varied from 30.3 per cent to 11.49 per cent. The leaves of pines which are destitute of silica in spring are rich in autumn. This rule about the oldest parts being richest in silica is not, however, without exception—the chaff of cereals and the seeds of Coniferæ being richer in silica than the stem, leaves, or wood. Kindt, Wicke, and Mohl have also demonstrated that the hairs of nettles are highly silicious. The permanence of the bark of some trees has even been attributed, according to Johnson, to the silica in it. The bast fibres of common hemp, manilla hemp (*Musa textilis*), aloe hemp (*Agave Americana*), common flax, and New Zealand flax (*Phormium tenax*), all contain much silica. In jute (*Corchorus textilis*) some cells are partially incrusted also; so that Wicke suggests that the durability of textile fibres "is to a degree dependent on their content of silica." From the great variability observed in the same plant as to the percentage of silica, it would seem in part to be an accidental ingredient of the vegetable kingdom; and evidence is not wanting in the experiments of Sachs to show that it is not a necessary ingredient to the prosperity of all plants—maize, for instance. Plants have been grown successfully without silica by Sachs, Knop, Nobbe and

---

[1] Wicke, Hinneberg's Journal, 1862, p. 143.

[2] Phil. Trans., 1790 and 1791.

Siegert, Stohmann, Rautenberg and Kuhn, Birner and Lucanus, Leydhecker, Wolff, and Hampe, some of whom have shown that the amount of silica in a plant may be increased or diminished artificially. It thus appears that "very little will suffice their needs, and highly probable that it is in no way essential to their physiological development," and "that the notion attributing the 'laying' of corn to a deficiency of silica in the straw is highly erroneous."

The unqualified truth of the very generally accepted idea that the use of silica is to give rigidity to the stems of plants, and so enable them to bear the weight of the fruit, is embarrassed by the fact that the silica is not always found in those parts of the plant which on this idea most require it, and that the lower sheathing part of the leaf of most cereals and grasses conduces as much to the support of the plant as the stem itself.

The idea that the stiffness of the straw depends on silica is not altogether true; and the theory that silica applied to crops will strengthen the stem, and keep them from "laying," is founded on an erroneous idea of its function in plant-life, which function is not yet settled.

Lithium (Li.), *Fluorine* (F.), *and Titanium* (Ti.)—Salm-Horstmar considered that a minute quantity of these elements was necessary to the fruiting of barley, and the same observer considered that a trace of *titanic acid* is also a necessary ingredient of plants. Later observations rather go to demonstrate the fallacy of this idea; but it is just possible, as Mülder has suggested, that exhaustion of soils is sometimes due to the exhaustion of some of the less abundant and usually overlooked ash ingredients.

Rubidium (Rb.) has been found in sugar-beet, tobacco, coffee, tea, and grapes, and along with *Cæsium* (Cs.) is most likely present in many other plants. Probably they may help the growth of plants, yet Birner and Lucanus declare that when potash is absent they act as a poison on the oat-plant.

Zinc (Zn.)—Alexander Braun and Risse show that zinc is an ingredient of plants in the vicinity of zinc-mines, where the soil contains a carbonate or silicate of that metal. In the ash of *Thlapsi alpestre*, var. *calaminaris*, Risse found 13 per cent of oxide of zinc, and in other plants from 0.3 to 3.3 per cent. It thus appears that the presence of this metal causes marked varieties in certain plants, as witness the variety mentioned and the var. *calaminaris* of *Viola tricolor*.

Copper (Cu.), *Arsenic* (As.), *Baryta* (Ba.), *Lead* (Pb.), *and Iodine* (I.), have all been discovered in the ash of plants; but what use they serve, or whether essential to all plants (Iodine appearing to be essential to many algæ only), is not certain, as indeed is also the history of the occurrence and use of the last ten substances mentioned, which, unlike the former five, can only be classed as accidental constituents of plants.

Karl Müller, in summing up the researches of Prince Salm-Horstmar on the food of the oat, defines the use of the different mineral ingredients in these words: "Without silicious earth, that plant cannot acquire sufficient strength to sustain itself erect, but forms a creeping stem, feeble and pale; without calcareous earth it dies even before the appearance of the second leaf; without soda and without potash it never attains a greater height than between 4 or 5 inches; without phosphorus, though growing straight and regularly formed, it remains feeble, and does not bear fruit; when iron is present in the soil it gives that deep-green tint so familiar to us, and grows rapidly robust; without manganese it develops in a stunted manner, and produces few flowers." How far this simple generalisation is correct, the student will have been able to judge for himself from the facts already stated.

Absorption of excess of Ash Ingredients by Plants.—That plants can take up more mineral ingredients than are indispensable to them has been long ago proved by the experiments of De Saussure, and more recently by other chemists. Saussure found that the ash ingredients of some peppermint plants in their normal state were 40.3 per cent, but that under artificial cultivation this increased in 2½ months to 62 per cent; so that it follows that the surplus was in excess, and accidental.

It has also been shown that the ash ingredients of a plant may be increased artificially. These superfluous ash ingredients, Johnson shows, may be disposed of variously: (1.) They may remain dissolved in and diffused throughout the juices of the plant; or (2.) exude from the surface as efflorescence, and be washed off by the rains, the latter appearance being repeatedly observed in the case of cucumbers and other kitchen vegetables. Saussure also found that "foliage readily yields up saline matters to water" if immersed in that liquid. By this treatment hazel-leaves lost in eight immersions of 15 minutes each $\frac{1}{15}$ of their ash ingredients. (3.) These insoluble matters may be deposited in crystals in the cells, or may incrust the cell-wall, and thus be set aside from the sphere of vital action, as in the case of cystolithes of sulphate of lime, &c., in many plants, which have been already noticed. (4.) Some plants absolutely excrete mineral matters, as is the case with *Saxifraga incrustata* found in lime soils, the leaves of which are "entirely coated with a scaly incrustation of calcium carbonate, mixed with some magnesium carbonate. At the edge of the leaf this incrustation acquires a considerable thickness." Unger found that the undried leaves yield 4.14 per cent of carbonate of lime, and 0.82 per cent of carbonate of magnesia. The same botanist found that this excretion of carbonates "proceeds mostly from a series of glandular expansions at the margin of the leaf which are directly connected with the sap-ducts of the plant."[1]

How the Ash Ingredients exist in the Plant.—This is not exactly known. In some plants (*e.g.*, oat) much of the ash matter is in a soluble form; and in the clover, the ash matter, according to Hellriegel, is more soluble in the young than in the old plant. Sulphates also may be absent from the *plant*, though present in the *ash*. Arendt found no sulphates in the lower joints of the stem of the oats after blossoming, though in the upper leaves at the same period there was present 7 per cent of sulphuric trioxide (SO_3). There are many similar instances.

To sum up the result of our inquiries regarding the use of the mineral ingredients of plants, we may say in a sentence that though the subject is yet involved in doubt, the use (1.) of the sulphates is to produce the albuminoids and the sulphurised oils of the onion, mustard, horse-radish, turnip, &c. (2.) That the use of the phosphates is to elaborate the phosphorised oils; and when found in the cereals, the explanation of their presence is, that "the soluble albuminoids which are formed in the foliage must pass thence through the cells and ducts of the stem into growing parts of the plant and into the seed, where they accumulate in large quantity." But as the albuminoids penetrate membranes with great difficulty and slowness in the pure state, potassium phosphate considerably increases the diffusive rate of albumen, and thus facilitates its translocation in the plant. (3.) The alkalies and alkali earths are concerned in the formation of organic acids (Johnson). We are, however, yet in the dark as to why no vegetable cell can be formed without lime or potash; or why magnesia, lime, or almost any other substance, is essential to the life of the vegetable organism.

COMPOSITION OF THE PLANT IN SUCCESSIVE STAGES OF GROWTH.

Professor Johnson, in his work on the chemistry of plants, devotes considerable space to this subject, narrating at length the researches of Norton, Arendt, and Bretschneider, chiefly in relation to the composition of the oat-plant. In a botanical work it is unnecessary to go at any length into this question, further than to refer the student to this treatise for details which may concern him as an agriculturist or a chemist. So far as the botanist is concerned, the general facts may be summarised as follows: Plants alter in composition as they develop. The observers named divided the growth of the oat-plant into five

---

[1] Sitzungsberichte der Wiener Akadam., 431, s. 519 (*fide* Johnson).

periods: the 1st being 18th or 19th June; the 2d, between June 30th and July 10th; the 3d, July 10th and July 21st; the 4th, between July 21st and July 31st; and the 5th and last, between July 31st and August 6th,—when on an average of the different observations the grain had ripened. It was found that the total weight of the crops increases in the first three periods, then lessens. The total weight of dry matter increases through the whole season, but the water of the crop lessens during the fifth period only. The period of blossoming is the period of most active growth. "Afterwards the rate of growth diminished by more than one-half, and at a later period increased again, though not to the maximum." The proportion of volatile to non-volatile matters varies slightly with the growth, and it was found that "plants produce more amyloids and less albuminoids as they matured. In other words, the plant requires a change of diet as it advances in growth." The daily increase was most marked when the plant was "heading out," or getting into ear. The following table shows these facts in a graphic form. The quantity of each proximate element in the ripe plant is assumed as 100:—

	Fibre per cent.	Fat per cent.	Amyloids per cent.	Albuminoids per cent.	Ash per cent.
1st period, .	18	20	15	27	29
2d " .	81	50	47	45	55
3d " .	100	85	70	57	79
4th " .	100	100	92	90	95
5th " .	100	100	100	100	100

The gain during the period was as follows:—

	Fibre per cent.	Fat per cent.	Amyloids per cent.	Albuminoids per cent.	Ash per cent.
1st period, .	18	20	15	27	29
2d " .	63	30	32	18	26
3d " .	19	35	23	12	24
4th " .	0	15	22	33	16
5th " .	0	0	8	10	5

The migration or translocation of mineral ingredients from one part of the plant to another during the growth is very curious. For instance, it is shown that the growth of the stem, leaves, and ear, most probably takes place at the expense of the roots; and that a transfer of amyloids probably, and albuminoids certainly, goes on from the leaves through the stem into the ear. *Silica* and *chlorine* do not appear to be subject to any noticeable change once they are fixed in the plant. *Phosphoric pentoxide* on the other hand, passes rapidly from the leaves and stem into the fruit in the earlier and later stages of growth. *Sulphuric trioxide* migrates rapidly after the blossoming of the plant from the lower stem, which then contains none. "It is almost certain, then, that sulphuric trioxide *originates*, either partially or wholly, by oxidation of sulphur, or some sulphurised compound in the upper organs of the oat." *Magnesia* is translated from the stem to the upper organs, where it constantly increases in quantity. *Lime* is probably stationary; and, as far as *potash* is concerned, it is probable that, with the exception of a decrease in the ears after blossoming, there is no transfer to any other part of the plant.

SOILS AND ROTATION OF CROPS.

From what we have said, the student will see how important a bearing this has upon practical agriculture. Indeed it lies at the basis of all scientific horticulture and agriculture, and on it is founded the theory of manures and the rotation of crops. If we could certainly know with the utmost exactitude what particular substance or substances every plant required for its nutrition, then all we would have to do would be to supply the soil in which it was deficient by means of manures, or suit every crop to the particular soil, which by analyses we discovered was suited to its growth, from containing the substances necessary to the proper nutrition of the crop. Agriculture would become a science instead of a simple art, and from his laboratory the chemist would issue his directions to the farmer, who would perform mechanically what the science of his *collaborateur* had found to be necessary to the growth of his crops or the nutrition of his exhausted lands. This is exactly what of late years has been attempted; but the early dreams evolved by the enthusiasm which Liebig's researches a quarter of a century ago excited, have not grown into the substantial results which some at the first start imagined they would eventuate in. This is no doubt owing to our yet extremely imperfect knowledge of the subject; but at the same time there is something deeper than this, and which the progress of science will not put out of the way. The sooner chemico-agriculturists recognise that the life of the plant is not altogether under the influence of mere mechanical or chemical forces the better. There is a vital force at work, which no combinations in the laboratory can ever imitate. At best the agricultural chemist can only give materials for this vital energy to work on; and it is the intervention of this which has rendered the theories so carefully wrought out in the laboratory not always borne out by practice.

Soils are, as we will have occasion to notice in another section of this work, dependent on the disintegration of the particular rocks in the district where found; and hence argillaceous, silicious, marly, calcareous, and loamy, according to the amount and character of the mineral ingredients of which they are composed.

Vegetable matter (or *humus*) enters largely into the composition of many soils, and has greatly altered their original composition. That plants can subsist, however, on mineral ingredients alone, is scarcely capable of doubt. The first plants most probably did so to a great extent, for of course vegetable *humus* could not exist before the materials of which it is composed did. We have, however, now got to the limits of our department. To enter upon the subject of soils or their formation, manures, or any other of the endless questions which lie contiguous to or dovetail into our science, would be foreign to our plan, and belongs to the department of agriculture rather than to scientific botany.[1]

Having now considered, so far as is necessary, the question of the chemical constituents of the plant and of the soil, we are prepared for entering on a consideration of how these materials find their way into the plant in the process of NUTRITION.

---

[1] Those who wish to refer more fully to the facts of which an outline is stated, will find them in by far the best work on the chemical history of plants—Professor Johnson of Yale's 'How Crops Grow,' edited by Professors Church and Dyer (1869), and in the various works and papers so abundantly quoted there; Boussingault's Economie Rurale, 2 vols.; Bibra, Die Getreidearten und das Brod (1860); Liebig's Agricultural Chemistry (Engl. trans.), and Ernährung der Vegetation; Arendt, Das Wachsthumder Haferflanze (1859); Wolff, Die naturgesetzlichen Grundlagen des Ackerbanes; Salm-Horstmar, Versuche und Resultate über die Nahrung der Pflanzen; Schulz-Fleck, Der Rationelle Ackerbau; Knop, Lehrbuch der Agricultur Chemie; Mülder, Chemie der Ackerbrume; Stöckhardt, Chemischer Ackersmann (1855); Wolff, Die Erschöpfung des Bodens dur die Cultur (1856); Johnston's Chemistry of Common Life, and Elements of Agricultural Chemistry; Falconer King, Trans. Highland and Agric. Soc. (1873); and the various papers of Hinneberg, Kohn, Aronstein, H. Schulze, Busse, Norton, Anderson, Voelcker, Péligot, Mitscherlich, Stein, Schacht, Bretschneider, Grouven, Sachs, Unger, Gladstone and Diver, Knop, Salm-Horstmar, Cloez, Stohmann, Metzdorf, Birner, Lucanus, Nobbe, Schmidt, Topler, Hoppe-Seyler, Ritthausen, Bopp, Pierre, Gorup-Besanez, Cohn, Maschke, Kubel, Hartig, Daubeny, and others: in the various volumes for later years of Jahresbericht für Chemie, Hinneberg's Journal für Landwirthschaft, Wilda's Centreblatt, Journal für Prakt. Chem., Versuchs Stationen, Annal. Chem. u. Pharm, Jahresbericht über Agricultur Chemie, Salsmünder Bericht, Sitzungsberichte der Wiener Akad., Transactions of the Highland and Agricultural Society of Scotland, Trans. of the Roy. Agr. Soc. of England, Silliman's Am. Jour. of Sc., Philosophical Transactions, Quarterly Journal of the Chemical Society of London, &c. &c.

CHAPTER V.

THE FUNCTION OF NUTRITION.

THE organs necessary for and concerned in the nutrition of the higher forms of vegetable life are, we have seen, the root, the stem, and the leaf. We have also seen that the plant increases in size and is composed of various chemical ingredients, which ingredients it must extract from the earth, air, or water, or from all three. Now the action of the root, stem, and leaf, in extracting these substances from the elements in which they are found, conveying them to the plant, and placing them so that they conduce to the increase and prosperity of the individual, constitutes the function of *Nutrition*. It is, in fact, the physiological action of the organs named in combination. Therefore, before dismissing this part of our study, let us consider this more as a whole than we have been able to do while mentioning the uses of the different organs concerned in it. Nutrition may be said to consist of seven different acts: 1. *Absorption;* 2. *Circulation;* 3. *Respiration*, or the elaboration of the nutritive fluid by the contact of the air and the exhalation of carbonic acid (carbonic dioxide);[1] 4. *Transpiration*, or loss of water; 5. *Excretion*, or elimination of substances injurious to the plant; 6. *Assimilation* of the nutriment; and 7.—its result—the *increase* of the organs.

In the most simple plants, such as the *Protococcus*, which is composed of a single cell—and even in some like the *Conferves*, which are made up of simple rows of cells—each cell seems capable of absorbing and elaborating the nutriment necessary for its simple organism (p. 14). In lichens, again, though simple cellular plants, there is most probably a different physiological function subserved by the outside green layer and the rest of the structure of the plant; but what this is we are yet entirely ignorant of. In the higher cryptogamia the case is different. Here the function of

---

[1] Here it may be mentioned that though the newest chemical nomenclature, such as is given by most approved authors, is followed, yet when a word is consecrated by long usage we may use it, even though not perfectly correct from the stand-point of scientific purism. Thus, carbonic acid is usually now called carbonic dioxide (CO_2).

nutrition is a much more elaborate operation; and in the Dicotyledons, owing to various circumstances, it has been more carefully studied than in the Monocotyledons. We shall therefore, in the observations which follow, describe it as it exists in the former division of plants. The nourishment is absorbed from the soil in a state of solution; from the root it passes into the wood, and thence into and through the stem and branches. From the stem and branches it flows into the leaves, and thence into their parenchyma, where it is subjected to the action of the air, evaporation, and other agencies which fit it for the nutrition of the plant, which previously it was not. In the first case it was *crude* sap;[1] it is now, after undergoing this elaboration in the leaves, *elaborated* sap. From the leaves the sap flows back again in the direction of the root through the bark, forming in its downward course the cambium (p. 89), out of which the young wood and the tissues generally are formed. In the course of its downward path it deposits in various portions of the plant stores of nutritive material, which again in the spring the ascending sap dissolves and carries onward for the nutrition of other portions of the plant. Thus it passes in its downward route transversely, depositing stores of starch in the medullary rays of many plants; so that, though its general course may be perpendicular and downward, yet it makes frequent transverse detours—"not indeed in determinate vessels, but in a definite path leading through the different parts of the plant." Having thus taken a glance, *tout ensemble*, at the functions of nutrition, let us consider it, in its individual phases, more in detail.

ABSORPTION OF NUTRITIVE FLUID.

In the preceding chapter we have seen that the various substances composing the tissues of the plant are derived from the air, earth, and water—more especially from the first two. All those derived from the earth are found in the ash. Those from the air, being gaseous, are naturally not found in the ash, but are determined to be present through other and more delicate means. Of these latter elements, oxygen alone is taken into the plant in a pure state; the rest are the result of certain chemical decompositions going on in its tissues. All the materials which the plant requires for its nourishment must be taken up in either a *liquid* or a *gaseous* condition—nothing solid, no matter how minute its subdivision, can be taken up by the plant.

It is, however, dubious, whether it is absolutely necessary for the nutritive substances to be in an inorganic form. On this there

---

[1] Also styled the non-elaborated, ascending, or spring sap, or sometimes simply *the* sap.

has been no little controversy. On the one hand it is pointed out that plants can derive nourishment in soils where absolutely nothing but inorganic substances can exist. Thus plants have grown, no doubt in a very stunted condition, and have even flowered, in sand which had been subjected to a red heat, and, according to Humboldt's experiments, even in a soil composed of metallic oxides, red oxide of lead, &c. Sukkow grew "salad plants" in pounded fluorate of lime and baryta. In powder of coal and sulphur seeds germinate likewise very well. Boussingault grew plants to maturity in soils which had been deprived, by being subjected to a red heat, of every trace of organic matter. In practice the same has been found true. In the interior of Peru and Chili rich harvests of maize are grown on soils of quicksand never enriched by manure; and, according to Campbell, the soil of the cinnamon gardens at Colombo, in Ceylon, is "pure quartz, and white as snow." The oil-palms of West Africa grow in moist sea-sand; and yet in nine years there was imported into England alone 107,118,000 lb. of palm-oil, containing 32,000 tons of carbon, furnished by a soil practically free from organic or carbonaceous matter of any sort.[1] On the other hand it can never be doubted that all plants cannot live on inorganic substances, or even, as Ingenhouz and more lately Liebig taught, require them for their nutrition. Thus a great number of plants, and even whole orders, like the Loranthaceæ (Misletoes), are parasitic on other plants, and must derive their nourishment from the juices of such plants, and of course imbibe a considerable amount of organic matter. Again, fungi, many bog-plants, orchids, &c., derive their nourishment from the decay of animal or vegetable substances alone. Lastly, it is pointed out that most plants, if deprived altogether of organic nutrition—as when grown in sand deprived by heat of any such matters—exhibit a stunted growth. Different plants, however, manifest in this respect widely different necessities. Firs, buckwheat, *Spergula*, *Sarothamnus*, *Erica*, *Calluna*, &c., can flourish in a soil which contains a mere trace of inorganic matter. Others, like all the cereals, require for their proper growth a certain amount of organic matter in the soil. The plants which grow in the great primeval forests must of necessity grow in a soil composed almost entirely to the depth of many feet of nothing but mould, formed out of the shed leaves and decayed tissues of thousands of generations of forest-trees and other plants. In fir forests of this type, generally very few species of plants grow under the shade of the trees—a fact probably due to the absence of light and inorganic matter, required for the growth of many plants, and the presence of resins in the vegetable mould. It thus appears that both organic and

---

[1] See Odling on Food of Plants, in Manchester Science Lectures for the People, 1871.

inorganic materials are required, and are capable of nourishing certain species of plants.

From whatever source this nutritive fluid is taken into the plant by means of the root, from the medium in which these roots are placed, it constitutes the *sap*. The *force* of the ascent of the sap into the roots and up the stem is very great, though this varies according to the hygroscopic character of the soil. Hales's experiments made more than 140 years ago,[1] which were mentioned when describing the functions of the root (p. 139), are still our best authority on the subject. Without even the force of argument derived from these experiments before us, it will be at once self-evident to the student that the force of the sap must be great to raise it against the force of gravity to the top of a palm-tree 200 feet, or of a *Sequoia* between 300 and 400 feet in height. Mohl, indeed, is inclined to attribute the imperfect nutrition which the terminal shoots of such trees must latterly get, from the increased difficulty year by year of the sap ascending to such a great height, as one of the chief causes of their decay and death.

The *rapidity* of ascent is also great; but this varies with heat, cold, the amount of moisture in the soil, and the dryness of the air. The mean velocity Dr M'Nab has calculated to be .0047292 inches per second—a result which gives a velocity greater than Hales or Sachs calculated.[2] The leaves assist by evaporation in the rapidity of the ascent. The leaves themselves are *not*, it may be mentioned, contrary to the common doctrine on the subject, organs of absorption of moisture from the air, though, if bathed in water, they will mechanically by endosmose absorb water.[3] However, while growing free in the air they only favour the plant in the way of moisture by arresting evaporation, not by directly absorbing moisture. *Inter alia*, it may be pointed out, as a proof of the all-powerful effect of the leaves in promoting the ascent of the sap, that if the shoot of a vine growing in the open air is put into a hothouse, the leaves will unfold, owing to the increased temperature, and immediately the sap will commence to rise, as it would have

---

[1] *Vegetable Staticks;* confirmed and extended by Brücke (in Poggendorf's Annales, 1844, No. 10), Mirbel, Chevreul, Hoffmeister, and others.

[2] Trans. Bot. Soc. Edin., xi. 29.

[3] Bonnet found that plants of *Mercurialis* absorbed as much, and kept nearly as fresh, when their leaves were in contact with water, as the same plants with their roots immersed. The hairs on the under surface of leaves act like the hairs of the rootlets in absorbing moisture. Hoffmann (Scientific Memoirs, i. 46) proves that after every fall of rain or dew, the leaves absorbed moisture, which, passing down into the tracheary vessels, &c., containing air, displaced for a time the air usually found in these vessels. Leaves have thus some analogy with roots—an analogy still greater in aerial roots which serve the purpose of leaves, and even throw out leaf-buds.—See, on the absorption of water by leaves, Cailletet, Ann. des Sc. Nat. Bot., ser. 5, xiv. (1872).

done had the leaves expanded naturally. All these facts confirm us in our ideas, derived so long ago from Hales, that the sap is active in proportion to the number of leaves on the plant. This leads us to ask, How is the sap absorbed by the roots? This question we partially discussed in chap. ii. (sect. ii. p. 138), when speaking of the functions of the root. We can now speak of it in more general terms, and from a wider stand-point.

This we saw was done by endosmose (p. 36) in the delicate cellular portions of the roots. In cellular plants the absorption of fluids takes place by the whole surface of the plant: and in those which are rooted like the Algæ, the root absorbs no nourishment in the same sense that the roots of the higher plants do; it simply acts as an anchor. In the higher plants, only the young rootlets absorb; if the young rootlets are kept from the soil or other nutritive medium, the plant will soon get sickly, even though the older roots are placed in a position to nourish the plant. Endosmose and exosmose can be seen if cellular tissue is laid in gum-water; the cells will gradually empty of their protoplasm, the gum being denser than the protoplasm inside. Again, if laid in water, they will, unless the cell-wall is very strong, burst, from the rapid absorption of water. In cells exist all the conditions necessary for endosmose,—viz., an organic membrane (the cell-wall), freely penetrable by water fluids; and in the cell-contents on one side of this membrane, dextrine, sugar, &c.; while on the other or outside, is the water occurring in nature, holding in a diluted solution certain saline substances. The result is that endosmose goes on with ease and rapidity. But if a root is put into food ready prepared for it—*e.g.*, gum, syrup, &c.—the result is that nutrition is retarded rather than assisted by endosmose being prevented. Roots will absorb no insoluble material, no matter how minute it may be. For instance, if silica is so minutely pulverised as to be suspended in syrup, not a particle will be absorbed. Even charcoal, so finely divided as it is in gunpowder, cannot be absorbed, even though mechanically suspended in water. The water will be absorbed, but the charcoal will be left behind. De Candolle found that the colouring matter of logwood, an infusion of saffron, &c., would be absorbed. But this was not by healthy roots; only by cut surfaces at the places where the plant had been wounded, and, accordingly, where the natural root-action of endosmose was not going on. Some substances are absorbed much more readily than others, even though these substances may be more fluid. Hence it is owing to this that plants have the power of selection. If the cells of the root are diseased, owing to the disturbance of the laws of endosmose, often more of some substance is taken up than would occur in the natural condition of the organ. The experiments of Trinchinetti are in opposition to those of De Saussure, in so far as they show that different substances are not absorbed by different plants in equal relative quantities. For instance, *Mercurialis annua* and *Chenopodium viride* absorbed much nitre and little salt (chloride of sodium), while *Satureia hortensis* and *Solanum Lycospersicum* took up much salt and little nitre. Again, from a mixture of sal-ammoniac and common salt, Mercurialis absorbed more sal-ammoniac, while *Vicia Faba* took more salt. Daubeny found that Pelargoniums, barley, and winged pea (*Lotus tetragonolobus*), though made to grow in a soil containing nitrate of strontia, absorbed none of the earth—at least none was found in the roots or stems when burned—thus confirming the experiments made by De Saussure on *Polygonum persicaria*, which refused to absorb acetate of lime from the soil, though it freely took up common salt; though, on the other hand, Gyde found that beans took up both lime and strontia without injury, if the substances were sufficiently diluted.[1]

Pure water is absorbed more readily than when substances are dissolved in it. It is possible this is owing to the peculiarity that the plant can reject substances in solution and only take up water. Fungi have been observed in arsenical solutions. Now arsenic is a substance so fatal to vegetation that it is scarcely possible to believe that any of it could have been absorbed by the plants. *Cereus variabilis*, after having been watered for ten weeks with a solution of sulphate of copper, took up no copper; and the same is true of *Stratiotes aloides* (water-soldier) and *Chara vulgaris*, both of which refused to take up copper—even though, as in the case of the latter plant, it vegetated for three weeks in a solution of the sulphate of that metal.[2] De Saussure considered that this selective power was owing simply to the different degrees of viscidity in the substances absorbed or rejected. But even could we conceive any sieve so fine as the one he imagined the delicate rootlets to be, recent experiments have distinctly shown that the capacity of plants to absorb certain substances in preference to others does not run parallel with the fluidity of these substances. Poisons are sometimes absorbed by plants. This seems contradictory of the views enunciated in the preceding paragraphs. On the contrary, however, there is nothing in this to cause us to doubt the selective power of roots. It is probable that the effect of these poisonous substances is to deaden the selective power of the rootlets, and so cause them to take up substances they otherwise would not, or more than their normal quantity. It is well known that plants which grow side by side in the same soil take up different substances—as is seen by the different analyses their

---

[1] Prize Essays, Highland and Agric. Soc., 1845.

[2] Vogel in Erdmand & Marchand's Journal, Bd. xxv. s. 209.

ash gives. This can only be explained in the light of the facts mentioned—viz., that roots have a selective power, and take up different constituents in an unequal quantity from the same solution; for Liebig's idea, that the roots are mere sponges taking up all presented to them, and again rejecting what they do not require, based as it was on Macaire-Prinsep's experiments, to be presently discussed, has not been borne out by late experiments and observation, though long a familiar doctrine among agriculturists.[1] No doubt when the leaf falls, some substances are returned to the soil; but this can only act in perennial, not in annual plants.[2] It is not, however, very easy to examine the function of absorption, except when the plant is grown in solutions in glass vessels; and even then it is so modified by various circumstances, such as evaporation, the different degrees of concentration of the sap, &c., that a wide field, and one of immense scientific and practical importance, lies before the experimenter on this subject.

CIRCULATION—ASCENT OF THE CRUDE SAP.

The nutritive fluid having now entered the plant through the rootlets, commences its circulation under the name of the *sap*. It is, in fact, only the water of the soil in the vicinity of the root, with the inorganic materials there found dissolved in it. Here it describes two courses—viz., an *ascending* and a *descending* course: the ascending course *to* the leaves, where it is submitted to certain influences which fit it for the nutrition of the plant; the descending one *from* the leaves, in a condition fitted for that purpose. Before, therefore, considering the descending sap, it will be necessary to describe the ascending one, and the processes it undergoes in the leaves (respiration and transpiration) before it becomes fit to descend and nourish the plant.

Composition, &c.—The sap begins to ascend in the spring when the soil is warmed. It cannot, of course, ascend when the soil is

---

[1] Bouchardat (Comptes rendus, 8th June 1846) also considered that roots would absorb anything presented to them in a liquid form; but he also believed that there were root excretions of a different kind in different plants. However, observations made by Cauvet in 1861 almost conclusively point out that he and others who adopt the doctrine of the non-selective power of roots and of root excretions were wrong, and that healthy roots would not absorb poisons, but if injured, they would do so. Nevertheless, if the plant survived the action of the poison, the leaves in which it concentrated died one after another. According to Liebig and Way, the roots do not find the materials of nourishment dissolved in the water of the soil, but excrete the carbonic acid which renders the substances soluble.—See p. 268.

[2] Mohl, Vegetable Cell (Henfrey's trans.), p. 69.

frozen, because at that time the moisture in which the nutritive materials require to be dissolved is in the state of ice. At this season the sap is liquid, and more or less limpid, and generally tasteless or insipidly sweet, though analyses show that it has an admixture of sugars, gums, albumen, and gluten, in addition to the salts which it holds in solution. The composition varies in different plants, as might naturally be expected, from the varying materials each plant takes from the soil. Invariably, however, the crude sap is of low density, water forming its great bulk, in which inorganic matters are dissolved often to a very small extent. The density of the sap of the vine, for instance, at the time of its greatest abundance, is only, according to Brücke, 1.001; while that of the elm, according to Vauquelin's analyses, is not more than 1.003—1.000 being taken as the standard of water. The proportion of the various substances dissolved in it increases as the sap ascends and the circulation goes on, on account of the supplies of starch, sugar, &c., deposited in the tissues of the plant during the preceding years being dissolved and taken up in the course of the circulation. The wood of all deciduous trees contains more or less of starch, and yields a sweet spring sap, produced, as in the case of the sugar-maple, from the transformation of this starch into sugar; while evergreens contain little or no starch.[1] Accordingly the sap varies in density as it ascends. Knight, and afterwards Biot, found, for instance, that in a maple the density of the sap in the stem close to the ground was 1.004; at the height of 6 feet, 1.008; at 12 feet, 1.012. However, as the summer advances, the amount of these substances found in the sap decreases, and simultaneously its density. The amount of sap which flows may be judged when it is known that the cut stem of an ordinary-sized vine will "bleed" one pint in 24 hours, and a sugar-maple tree (*Acer saccharinum*) 200 lb. in the course of a season—this amount of sap holding about 10 lb. of sugar in solution. In palms and some other tropical trees the sap ascends continuously all the year through; but in all the plants of our northern and temperate latitudes it only ascends in the spring (or perhaps in some cases to a slight extent in the autumn), when it bursts the buds open, and then, the leaves expanded, the circulation goes on apace. Cold stops it; and hence a cold spring stops by this means the bursting of the buds, and thus checks vegetation.

The effect of heat or cold is well seen in the flow of sap from a sugar-maple during the season when it is collected for the sake of its sugar. During warm dull nights the radiant heat of the sun is most rapidly absorbed by the dark rough surface of the tree; then the temperature of the latter rises most speedily, and acquires

---

[1] Hartig, Journ. für Prakt. Ch., v. 271 (*teste* Johnson, l. c.)

the greatest elevation—even surpasses that of the atmosphere by several degrees: the sap at that season is also most copious. On the contrary, on clear nights the cooling of the tree takes place with corresponding rapidity; then the snow or surface of the ground is frozen, and the flow of sap is checked. From trees that have a southern sunny exposure, the sap runs earlier and faster than from those which have a contrary aspect. Sap starts sooner from the spiles on the south side of a tree than from those towards the north (Johnson). Sometimes the sap will commence to flow when the snow is on the ground. In that case the deep-seated roots must be sufficiently warmly placed to allow endosmose to commence, and the trunk sufficiently warmed by the sun to allow it to flow.

Path of ascent.—Regarding this there are two rival theories—viz., one that it ascends in vessels (Malpighi, Duhamel, Treviranus, Link, &c., including all the older botanists), and the other that the vessels are reserved for the conveyance of air while the sap ascends through the cellular or wood tissue (Schleiden, Mohl, &c.) Accordingly, the vessels have been called *air* or *sap* or *lymphatic* vessels, in accordance with the opinion, as to their function, of the particular writer quoted. The truth may probably be found, as it is usually, somewhere midway between these rival theories. The outer and youngest layers of wood, and in stems not more than two years old the medullary sheath also, chiefly carry sap; but the older and harder wood takes less and less share in conveying sap. Hence the duramen or heart-wood carries none; while in soft-wooded trees like the poplar and willow the centre wood still conveys sap, as perfectly as does the albumen of hard-wooded trees. In spring, however, the whole plant gets so gorged with sap that the vessels are also filled with it; it is only at this time that the sap flows from an incision in the wood. After the press of work is over, the vessels again resume their usual office of carrying air, and the plant settles down to its normal condition.[1] Sachs has shown that though the sap in the parenchyma and that in the vessels are not invariably distinct one from another, yet in most cases the cellular tissue contains chiefly nitrogenous principles (sugar, starch, oil, &c.), and also organic acids and acid salts, which give a red colour to litmus paper; while the vascular tissue contains a preponderance of albuminoids, and gives an alkaline reaction. This exceptional spring condition of woody plants in our climate is a normal one in certain tropical climbing plants called

---

[1] Link, Ann. des Sc. Nat., xxiii. 144; Vorles über Kräuterkunde, vol. i. s. 116; Rominger, Bot. Zeit., 1843, s. 177; Mohl and Hoffmann, Bot. Zeit., 1850; Scientific Memoirs, ser. 2, vol. i.; Schleiden, Grundzüge der Wissenschftl. Botanik, 2 Auft. Bd. ii. s. 505; Hoffmeister, Flora, 1858, ss. 1-12 (trans. in Ann. des Sc. Nat., x. (1858) 5-19).

"Lianas," (p. 112, 136), especially in Phytocrene and certain species of *Cissus*.[1]

However, in Coniferæ, in which there are no vessels, the wood-cells must alone convey the sap. In these and other woody plants the sap can easily enter, owing to the numerous punctations or thin places in their walls. Indeed, Hoffmeister tries to demonstrate that the wood-cells are much more permeable than the cells of the parenchyma itself.[2]

Lateral movement.—When the sap arrives opposite the leaves, it sends off lateral branches, which direct a sufficiency of sap into the bundles of vessels, &c., composing the petiole, and from which it circulates by means of the ribs and veins all through the leaf, and finally passes into the parenchyma. The sap thus, though describing a *general* upright course, in reality takes a more or less zigzag path. At this time the bark is easily torn off.

Autumn sap.—Occasionally, under exceptional circumstances, there will be an ascent of the sap for a brief period during the autumn, just before the plant has gone into the dormant condition its vital functions are in during the winter months. Leaves, before they fall, develop buds in their axils. These buds, therefore, sometimes stimulate another ascent for a short time, until it is stopped by the winter cold. In early-leafing trees (poplars, lindens, &c.) it is chiefly seen, and most frequently after a hot, dry summer, when the leaves soon fall; when, if succeeded by plentiful rains and a warm autumn, the sap rises. Perhaps errors in determining the age of trees by the rings of wood may be made in this way, since the short autumn ascent will also form a thin layer of wood. This autumn ascent is not, however, by any means a general occurrence in our climate.

After this fitful revival of circulatory life, the vital forces of the plant languish, and finally go into a state of winter repose. There is, however, always more or less of water in the stem of trees all the year round, ranging, as in the case of the beech, from 35 to 49 per cent—the minimum, however, being found during the summer months, the maximum in December and January. This water is owing to the fact that in the autumn and winter, so long as the weather is mild, the roots continue to absorb the nutritive fluid around them. The leaves having perished, this sap is not elaborated, but deposits in the tissue its inorganic contents, which, undergoing transformation during the winter into starch, &c., are again, as we have already mentioned, redissolved in the spring by the ascending sap, to be carried on to aid in the nutrition of the plant.

---

[1] Gaudichaud, Ann. des Sc. Nat., 2d ser., vi. 138; Poiteau, Ann. des Sc. Nat., vii. 233.

[2] Flora, 1862; Nos. 7, 8, 9, 10, 11.

In warm climates there is a different state of affairs. In tropical countries there is little or no cessation of the circulation, on account of there being little, if any, difference between the different seasons of the year. Accordingly, many trees of such climates are without "annual rings" of wood. In palm-trees the juice is so rich in nutritive saccharine materials that it is boiled like that of the sugar-maple in order to extract the sugar. In certain tropical climbers we have already mentioned that the plant is gorged with sap all the year round, and that sap can be got from them at almost any time of the year. Hence travellers in tropical forests take advantage of this to quench their thirst. On this account some of these species (such as *Cissus hydrophora*) are known as the "water" or "Hunters' Lianas." Here a curious observation made by Gaudichaud[1] on this species of *Cissus*, and by Poiteau on another but unknown species of the same genus, may be mentioned. If the stem is cut across at one place only, very little sap issues from the two cut surfaces (the upper and lower). "It continues to mount rapidly in the upper part, in which we may be assured that the vessels are being emptied from the bottom to the top. The ascension cannot be attributed to the roots, with which the upper part is no longer in connection, and the vessels are of much too large a diameter for capillary attraction to have any influence. But if we cut it at two different heights, so as to detach a fragment of the stem of a certain length, we immediately see a great abundance of sap flow from that extremity which is held the lowest down, consequently obeying the laws of gravity. Now previously the sap continued to mount very rapidly. This can be caused by no force which is placed beneath or at the sides; it can only, therefore, be from some force situated above the second section, and drawing the liquid upwards."

In the course of the ascent, the sap, as we have already intimated, changes rapidly in composition. The stem is the scene of busy chemical activity, and within this organic laboratory numerous physical, vital, and chemical processes are going on, the results of which are, that the sap mixes with and takes up the substances deposited during the previous year, and so changes its composition until it arrives at the leaf, when still further and more important changes take place.

The method in which heat expedites and cold retards the circulation seems to be simply by the mechanical operation of contracting or expanding the cells and vessels.

Causes of the ascent of the sap.—This is a subject of much interest and no little controversy. Here we see a fluid ascending, contrary to the laws of gravity. What, then, are the causes that enable it to rebel against the laws of nature in order to fill its place

---

[1] L. cit.

in the economy of nature? On studying the matter closely, it will be seen that this cannot be explained by one set of causes alone, but by many, often widely different, and seemingly disconnected. These causes may be classified as follows:—

1. *Endosmose.*—This, the initial force, we have already discussed (p. 36).

2. *Capillary attraction.*—This has a considerable influence on the ascent of the sap, and is the *rationale* of several familiar horticultural operations. For instance, this is the reason why gardeners cut off the rootlets to "refresh" a plant when withered. The delicate cells of the rootlets have lost the power of imbibing moisture by endosmose, but the physical operation of capillary attraction of moisture and nutriment through the open ends of the vessels still enables the plant to draw up sufficient to meet its wants, until it has recuperated itself and put forth fresh rootlets. When a "cutting" is put into the ground, the first moisture drawn up by it is through capillary attraction also. The horticulturist cuts the end which is to go into the ground in a slanting manner, not only for greater convenience in the mechanical operation of pushing it into the soil, but also that a greater exposure of the open mouths of the vessels may thereby be obtained, and the vessels not contract so easily. It is also by capillary attraction that a bouquet is nourished when the cut ends of the flowers are put into water.

When the vessels are cut across in this manner, then, and then only, will colouring matters enter the plant along with the water in which they are held in suspension or solution; and accordingly, advantage has been taken of this to trace the course of the sap. Experiments undertaken on plants in which the sap enters in this unnatural manner are, however, not to be implicitly relied on. Capillary attraction is well seen in the continuous ascent of oil in wick when at the same time the oil is withdrawn by supporting the flame at the other end. Something very nearly the same is seen in plants—the leaves, in this case, by their evaporating the drawn-up liquid, acting the part of the flame in the wick of the lamp.

3. *Evaporation by the leaves.*—In the course of the spring ascent of the sap, a time will come when endosmose will no longer act so readily, the equilibrium of the contents of the cells and the entering sap being restored, and when capillary attraction ceases to operate also. Yet we see a plant, after its full size has been attained, still drawing up moisture from the soil, as exemplified in the "Lianas" and suchlike plants (p. 112, 136). How is this? We answer, that the leaves, by exposing the sap to the air over an extended surface, cause much evaporation, as we shall presently see, and this evaporation acts as a *vis e fronte* to draw up more sap to supply that lost by this means, just as the water

entering by endosmose to supply the place of that transferred to those above them is a *vis a tergo*. There are thus two forces at work at either end of the plant, in addition to the capillary attraction in the middle assisting in drawing up the sap. The one is the root, which *pumps* it into the plant by means of endosmose; the other is the leaves, which *draw up* this pumped-in fluid. It is seen that the root attracts when the leaves do not, by the experiment of the sap of the vine flowing more forcibly when the root is transferred to a warmer temperature.[1] The sap flows then not only from the cut stem of the bleeding vine, but also from the most minute ramifications of the root. Even when there are leaves, the action of the root is also frequently necessary. This is shown by the leaves of *Nymphæa alba*, the white water-lily, and other plants, drying up when the stem is cut across, though placed in water; but if placed in water under similar circumstances, with the fibrils of the roots uninjured, the plant will remain fresh.[2] Yet the leaves, when even a small number only are left, can lift the fluid up to their level, as shown by the fact that pyrolignite of iron will rise in enormous quantities in the stem to the leaves if the extremities of the plant are placed in it.[3] Capillary attraction has, however, much to do with this. The effect of the leaves in attracting the sap is also shown by the fact, that as soon as the buds expand the ascent of the sap is rapidly increased, and by the experiment of the sap commencing to ascend if the bud is forcibly opened by being put into a hothouse; it is also shown when a graft has a different time of leafing from the stock on which it is grown, the graft in this case regulating entirely the season of the flow of the sap, and thereby influencing and controlling the habits and life of the stock.

---

[1] Dassen in Frorieps Neuen Notizen, Bd. xxxix. s. 129.

[2] The Nymphæaceæ grow larger, more abundant, and flower earlier, when grown in warmish water. In unusually hot summers, when the water in which they grow is diminished, or even altogether dried up, they grow with undiminished vigour, standing erect, though whether any change of structure takes place in the stem and peduncles to suit the new condition of life has not been ascertained. The stomata being only on the upper surface of the leaves, there is a curious provision to prevent the leaves being submerged by any increase of water in the pond or lake in which they grow. This consists in the stem not being straight, but bent; so in the case of such an emergency as the pond being flooded, it can straighten itself, and thus still keep its leaves floating. I question, however, if Mr Britten of the British Museum, to whom (Field Magazine, iii. 46) we are indebted for these facts, is right either in his facts or his explanations of them, when he says that fluid will not ascend in the stem on account of its being cellular and filled with air. Lecoq says that after the young plants are furnished with their primordial leaves they float about, following the course of the stream, entirely unattached to the soil; and the same fact has been observed in *N. tuberosa*, a North American species.

[3] Boucherie, Comptes rendus, t. ii. (1840) 897.

4. *The waving of the tree* or other plant by the wind, Mr Herbert Spencer has recently shown, assists mechanically in causing the ascent of the sap, by alternately compressing and relaxing the vessels.[1]

5. *Diffusion of liquids.*—This assists throughout in aiding the ascent of the sap, especially in conditions when it could not be accomplished either by the attractive power of evaporation of the leaves, or by capillarity. This is accomplished in virtue of the power which certain liquids have to pass through each other. The late Thomas Graham named the thin, readily diffusible liquids, such as the saccharose, glucose, and other such acids, and the ordinary salts, "crystalloids;" and from their gluey nature, the other less easily diffusible ones, like starch, the gums, gelatine, &c., "colloids." Now the "crystalloids" pass through and diffuse themselves among the "colloids," hence assisting in carrying forward the sap.

To these primary causes may be added the variations of temperature, especially in the spring, causing the vessels to alternately expand and contract, and so force up the sap, and the imbibition of the walls of the cells and vessels, owing to the porosity of vegetable tissues, and we have the most patent causes of the ascent of the sap. Boehm's idea,[2] that the sap ascends by atmospheric pressure, is not in accordance with known facts, and may therefore be at once dismissed from discussion.

The porosity of vegetable tissues is, however, only in reality a modification, though an important one, of capillarity, when a portion of parenchyma is subjected to great dryness, so that the contents would be evaporated. This, however, probably never in reality occurs, if the plant is in a healthy state; for instantly, by this modification of capillarity, the cell-wall of the dry cell would imbibe the juice from the neighbouring ones which are full, and simultaneously endosmose and exosmose would commence, and the sap accordingly ascend. It is thus a powerful secondary cause of the ascent of the sap, though probably Hoffmeister overestimates its influence when he considers it as one of the chief causes of the ascent of the sap in woody bodies. Assuredly Unger exaggerates its importance when he declares that

---

[1] Trans. Linn. Soc., xxv. (1866) 405-429.

[2] Sitzungsberichte der wiener Akad., &c. (1864). For a fuller description of the physical and physiological causes of the ascent of the sap than our space will admit of, the student is referred to Sachs' Experimental Physiology of Plants (either in German or French); Johnson's admirable treatise, already referred to and quoted; Hallier's Phytopathologie (1868); Schumacher's Physik der Pflanze; Dutrochet's various works; papers by Boehm in Sitzungsberichte, &c., 1863; Fr. Schulze in Karsten's Bot. Untersuch. ii.; Knight's papers on Vegetable Physiology; Herbert Spencer's Principles of Biology, &c.

sap does not ascend *within* cells or vessels, but simply by imbibition through their walls.

We have thus briefly but comprehensively given a summary of the phenomenon of the ascent of the sap, and the causes which are either conducive to this ascent, or are supposed to conduce to it. In reality, however, the cause of the ascent of the sap is by no means placed beyond a doubt, and, like a hundred other questions in vegetable physiology, is still open to farther examination. For instance, it seems one of the easiest things in the world to show how endosmose can go on in the plant in the way we have described. The fact is, that the stores of organic compounds, especially starch, are not contained in the wood-cells through which the sap chiefly ascends, but in the pith and medullary rays, or in the rind of the root; while in various monocotyledons, which, like the palms, lay up a store of sugar, gum, starch, &c., these substances are deposited in the parenchymatous cells of the stem. Therefore, though we can account for the sap entering the delicate fibrils of the root, we must coincide in Mohl's opinion that the method in which it reaches the wood-cells and vessels, and that in which the motion is imparted to it, notwithstanding the various explanations offered, are at present among the unsolved questions of Phyto-Physiology. No doubt we can account for the leaves attracting the sap by means of endosmose, on account of the thinner sap coming, in accordance with the physical law already described, to take the place of the thick sap concentrated by evaporation in the parenchyma of the leaf; but we cannot explain by endosmose why the ascending sap will ascend through the wood and vessels, and not by the bark, or why the descending sap takes a contrary course.

RESPIRATION.

Perhaps this is scarcely a correct word to apply to the phenomenon of the plant decomposing the atmospheric air, retaining certain portions to build up its tissue, and exhaling others by means of its leaves and green portion under the action of light, while it performs a contrary operation in darkness—in fact, a double respiration. The plant has no organs corresponding to the lungs or gills of the higher animals, but still the term is convenient as expressing an operation analogous to, if not homologous with, that performed by animals. The composition of atmospheric air is, nitrogen 79, oxygen 20, and a little carbonic acid, which is a compound of carbon and oxygen (CO_2). It is, however, in very small quantity. Nevertheless, it has been calculated that, though it only forms 1,000,000th part of the air, there are in the atmosphere 138,616,075,892 tons of carbon. This is being continually imbibed by plants during the day, and exhaled by animals, while volcanoes, decomposition of organisms, &c., are continually supplying it to the atmosphere. The stomata, and the epidermis when it is not too thick or indurated, allow the air to enter. The young branches, scales, twigs, &c., all act like leaves, absorbing air which ramifies through the plant probably by means of the spiral vessels, and into cellular passages. This operation consists essentially in taking in CO_2, decomposing it under the action of light, sending out the O., while the carbon is retained for the purpose of assisting in building up the tissues. The chief agent in this decomposition of CO_2 is chlorophyll. That O. is being given off can easily be seen if a few leaves are put into water, and the vessel covered over with a corked funnel. In a short time, under the action of sunlight, bubbles of oxygen will rise until the funnel is full. Then take out the cork, and the escaping oxygen will revivify a spark, or even cause a blown-out taper to burst into flame.[1]

In darkness the plant absorbs O. and gives out CO_2, but in smaller quantities. This CO_2 is probably derived from the combination of the O. with the carbon of the plant. Dumas and other chemists have, however, asserted that it is only the CO_2 drawn from the soil in the sap escaping from the plant undecomposed during the absence of sunlight. Certain experiments by Unger and others also show that probably the air is not alone the source of the carbon in the plant. The amount of O. absorbed in different plants in twenty-four hours varies from $\frac{1}{2}$ to 8 times the volume of the plant. All parts of the plant,—such as the root, woody stems, flowers,[2] buds;[3] Phanerogamia without chlorophyll, such as Orobanches, *Monotropa*, *Cytinus*, *Rafflesia*, &c.,[4] fungi,[5] &c.,—not coloured green, give out CO_2 in like manner, whether exposed to the light or not, though in varying quantity. Germinating seeds, in like manner, take in O. and give out CO_2. It is probable that this is the reason why the vitality of seeds can so long remain

---

[1] This method of demonstrating the emission of O. by the plant is, however, owing to the leaves being in a condition unnatural to them, liable to objection. It can be, therefore, equally well seen, and more naturally, if the somewhat more difficult method of experiment, on the leaves or the branch in connection with the plant, adopted by Boussingault (Economie rurale, i. 61), or by Rauwenoff, Vogel, and Witter (Mem. Acad. Munich, vi. (1851) 265-345), and others be adopted.

[2] Saussure, De l'Action des fleurs sur l'air; Ann. des Chim. et de Phys., xxi. (1822) 279-303.

[3] Garreau, Ann. des Sc. Nat., xv. (1851) 5-36, and xvi. (1851) 271-292.

[4] Lory, Ann. des Sc. Nat., viii. (1847) 158-172.

[5] Grischow, Physikalisch-chemische Untersuchungen über die Athmungen (1819), ss. 160-163.

dormant if they are buried in the ground and thus kept from air. It is perhaps somewhat theoretical, however, to attribute unhealthiness to places where there are many flowers, on account of their absorption of O. and disengagement of CO_2. Professor Kedzie, of the Michigan (U.S.) Agricultural College, analysed volumes of air taken at noon from different parts of the College greenhouse, containing 6000 plants, after it had been closed for twelve hours. He found the CO_2 amounted to 1.39 in 10,000 parts. A similar analysis of the air taken before sunrise indicates the CO_2 to have increased to 3.94 in 10,000 parts. Hence the accumulation of CO_2 was greater in darkness or during night than during the day—a fact in accordance with previous observation. However, ordinary country air outdoors contains four parts of CO_2 per 10,000; so that, even with all the plants in it, the air of the greenhouse was actually purer than it, and the emission of CO_2 was barely sufficient to counterbalance the production of oxygen during the day. This being the case where 6000 plants are collected, the harm done by a dozen or two in a bedroom must be inappreciable.

The behaviour of fungi is somewhat peculiar at all times. Sachs, for instance, thinks that they induce a marked exhalation of ammonia at the surface. Borscow[1] even affirms that the production of gaseous ammonia is a characteristic of the whole order, or at least of the Agarics—the quantity of gas exhaled being in proportion to the vital activity of the plant, but having nothing to do with its weight. It is equally without relation to the production of CO_2 as a result of respiration. Wolff and Zimmermann[2] object to these conclusions, and believe the small traces of ammonia they found in their experiments to be only a product of decomposition of the tissues, but a product which begins to appear immediately the vital functions of the organisms are slackened. With these conclusions we are inclined, from experiments made by us, to coincide. It is also almost certain that the traces of hydrogen which Humboldt considered fungi disengaged were only accidentally present in the air, having only been found in one case (*Amanita muscaria*), and never confirmed.

The CO_2 given out at night has been thought to be taken up by the roots mixed with the sap, though how the CO_2 can be taken up in this manner when the sap is not ascending, as is the case in our latitude for about one half of the year, is somewhat difficult to understand. The root, moreover, has not the power of absorbing much CO_2, as the experiments of Corenwinder prove. The respiration during the day has been called the *diurnal* or *chlorophyllian respiration*, chlorophyll being the agent chiefly engaged in caus-

---

[1] Mélanges Biologiques tirés du Bull. de l'Acad. Imp. des Sc. de St Pétersb., viii. 12.

[2] Bot. Zeit., 1871, Nos. 18 and 19.

ing the decomposition of CO_2; while to the second has been given the name of *nocturnal* or *general*, because it is common to all the organs of the plant, even to the leaves in the absence of light.[1] We may say, with Garreau and Sachs, that is the *true* respiration, the other being more an act of nutrition than true respiration, as we understand it in the higher animals.

It has been supposed by some physiologists that under exceptional circumstances—such as a clouded sky, &c.—plants even during broad day will inhale O. and give out CO_2, or at least form it, only to be speedily decomposed by the action of chlorophyll. But the experiments on this subject are too contradictory to allow us to form any stable conclusions regarding this important point.[2] The oxygen disengaged from plants under the action of sunlight varies in amount in accordance with the amount of light the plant is exposed to, and decreases in the shade.[3] Plants, however, which, like Coniferæ and others, grow naturally in the shade, are less sensible than others to light. Plants flourish in the dark shade of the dense primeval forests, and it is seen from the bright green of the leaves that they decompose CO_2.

Heat has also some effect on the evolution of O. by water-plants. Thus in certain experiments with the feather-foil (*Hottonia palustris*), Heinrich[4] found that if the plant was placed in common water at a temperature of 2°.7 Cent.—36°.86 Fahr.—in full sunlight, no evolution of gas took place, but at 5°.6 C. a regular evolution commenced. The most active period was when the water was at 31° C. At from 50° to 56° C. the gas ceased to be formed, but the leaf resumed its activity in cooler water. If the leaves were exposed to a temperature of 60° C. for ten minutes, their power of decomposing CO_2—and we suspect of performing any other functions too—was destroyed. The amount of O. exhaled also varies under illumination by different rays of the spectrum: under red there is none set free; in red and orange, 24.75; in yellow and green, 43.75; in green and blue, 4.10; in blue, 1.0; in indigo, 0,—the light acting according to the intensity of its illuminating power.[5]

---

[1] Mr Pepys probably stands alone in his belief that the evolution of CO_2 is only in an abnormal state of the plant (Phil. Trans., 1843, 339), though Draper maintains that plants, like animals, absorb O. and exhale CO_2—a deduction founded (in our opinion) on data too imperfect to admit of its being seriously discussed.

[2] For a discussion of the question, see Garreau, l. c.; Ed. Robin, Comptes rendus, 14th July 1851; and Mène in Richard, lib. cit., 149; Traube, Monatsbericht, &c., 1859, ss. 83-94 (Bull. Soc. Bot. Fr., 1859, 62, 63); and Sachs, lib. cit.: while the contrary view is taken by Corenwinder, Mém. de la Soc. des Sc. de Lille, 1863; and Ann. des Sc. Nat., 1864, 297-313.

[3] Though, curiously enough, Prillieux has shown that the viridescence of leaves is more rapid in diffused light than in the direct light of the sun.

[4] Journ. Chemical Soc., Nov. 1871.

[5] Draper, On the Forces which produce the Organisation of Plants, Appen-

Different species of plants vary also in their power of decomposing CO_2. Probably this is not related to anything in the constitution of the particular plants, but only to the form of their leaves. Thus Saussure found that very thin and particularly laciniated leaves exhaled more O. than others which exposed less surface to the atmosphere in proportion to their bulk. Fleshy leaves consume less O. and disengage less CO_2 than other leaves. In Saussure's experiments with 57 species of plants, the apricot and beech consumed most O. in darkness, and the *Agave Americana* (American aloe) and *Alisma plantago* (water-plantain)—the one a fleshy, and the other a marsh plant—least.

There is in general no fixed relation between the number and size of the stomata and the amount of gas disengaged,[1] though in some trees with a dry and coriaceous tissue there is a relation of this sort. Very young and tender leaves disengage little or no O.; but coriaceous and dry ones do in youth—hence they are soon consolidated. Fruits while green exercise, though in a less degree, the same respiratory functions as leaves; but as they ripen, this power gets gradually weaker and weaker, until finally, after they get ripe, it is entirely lost. Leaves cannot decompose pure CO_2 unless it is rarefied; and when it is mixed with nitrogen or oxygen they are equally incapable of performing that operation. The elimination of O. from growing plants is a chemical necessity when we know that the plant lives for the most part on oxygenated food. Hence, supposing starch to be formed by a plant from CO_2 and water, the following formula will represent the extrication of 12 atoms oxygen:—

$$6\,CO_2+5\,H_2O=C_6\,H_{10}\,O_5+12O \quad \text{(Johnson).}$$

When plants are continuously kept from light, their nutrition suffers; they become sickly, weak, and etoliated. As seen in the case of a potato kept in a dark cellar, they form shoots at the expense of the nutriment stored up in the older parts, these shoots being even of a larger size than similar ones formed under the action of light, but weak and soft. The leaves do not increase in size, do not become green, and the normal qualities of the saps are altered, bitter milky plants remaining sweet, &c. Some plants will exist

dix, 177. Pfeffer (Arbeiten der Bot. Instit. in Würzburg, Cahier I., 1871) concludes that "the rays of the spectrum perceptible to our eyes are the only ones which can become the cause of the decomposition of CO_2—the rays endowed with the most considerable illuminating power (the yellow rays) exerting themselves an influence equal to that of all the others taken together. The most refrangible rays possess a much less marked action. To each spectral colour there belongs a certain degree of activity in the phenomenon of assimilation—a degree which remains the same whether the rays act isolatedly upon plants, or whether their action is combined." See also Barentzky in Bot. Zeit., 1872, No. 13.

[1] Duchartre, Comptes rendus, xlii. 37.

for months in this sickly condition, but they cannot bear it permanently (v. Mohl). If, on the other hand, more than the normal quantity of CO_2 is supplied to the plant, it will flourish and increase its bulk greatly, even to an extent double that of the carbon contained in the inhaled CO_2.[1] On the contrary, all the functions of the plant become paralysed if placed in air containing no oxygen—*e.g.*, nitrogen. According to Dutrochet,[2] the unfolding of the leaf-buds is checked, resulting in them finally rotting; and the leaves no longer turn towards the light, or exhibit the alternate movement of folding and opening. Even single organs cut off from oxygenated air, like roots buried too deeply in the earth, decay and die. According to Saussure's experiments, a *Cactus*, one of an order usually very retentive of life, died in five days in non-oxygenated air. Yet the experiments of Messrs Gladstone[3] show that plants remained green and in good health during fifteen days in pure hydrogen, during almost three weeks in nitrogen, and even during four weeks in pure carbonic oxide (CO)—a gas eminently deleterious to animals which breath it. Boussingault[4] considers that he had detected marsh-plants exhale an exceedingly small quantity of this carbonic oxide; but the latest researches, those of Cloez,[5] give decisively negative results: so that this, like many other assertions we have touched on in this chapter, must receive the Scotch verdict of *not proven.*

Under the action of actively poisonous gases—such as sulphurous acid, hydrochloric, chlorine, and nitrous acid gases — the plant disorganises as if under the action of an irritant poison; while under the action of sulphuretted hydrogen, cyanogen, carbon dioxide, and ammoniacal gas, they droop and decay.[6] The action of sulphurous acid seemed to consist in its being converted into sulphuric acid by oxidation, and so attacking the tissues of plants. Coal-smoke injures plants chiefly by clogging up the stomata, and so impeding respiration and transpiration.

Oxygen, as we have seen, is the only gas which is taken into the plant in a pure state; the rest are in a compound form. For instance, the substances which give nitrogen are taken up by the roots, and not[7] by the leaves.[8] Nitrogen, it appears probable, from

---

[1] Saussure, Recherches, &c., 226.

[2] Mémoires, &c., i. 361, 483.

[3] Philosophical Magazine, Sept. 1851.

[4] Comptes rendus, liii. (1861) 882, 883; and lvii. (1863) 412-414.

[5] Ibid., lvii. 357.

[6] See the extended observations of Christison in Ed. Med. and Surg. Journal, xxvii. 356; and those of Livingstone and Coldstream in Edin. New Phil. Journ. 1859, and Trans. Bot. Soc. vi. 391 and 325 (on the effects of anæsthetics on sensitive plants).

[7] Comptes rendus, Nov. 28, 1853; Ann. des. Sc. Nat., ser. 4, t. i. and ii. (1854), and t. vii. (1857).

[8] Ville (Comptes rendus, xxxi. 678) tries to prove the contrary—viz., that it is absorbed by the leaves from the atmosphere.

the researches of Boussingault, Liebig, Lawes and Gilbert, and Pugh, is derived, not from the atmosphere, which it enters into the composition of to the extent of $\frac{4}{5}$, but from ammonia—ammoniacal salts being found in abundance in the ascending sap of the maple, birch, &c. Hence the value of guano and other manures containing ammonia. The universal diffusion of water will give hydrogen, while carbon and oxygen are supplied both from this and from the sources already indicated.

In Water-plants.—The air dissolved in water acts on water-plants not through the stomata, as in land-plants—these being wanting on the surfaces of aquatic plants exposed to water—but through their cuticle. They send out oxygen by both the upper and lower surfaces of the leaves (Duchartre). Water-plants get etoliated in darkness; yet, according to the experiments of Cloez and Gratiolet, no CO_2 is sent out under the action of darkness, though the decomposition of that gas is, as in terrestrial plants, affected under the action of light. Nevertheless—as shown by their experiments, and those of Heinrich, already quoted (p. 255)—a certain elevation of the temperature of the water is necessary for this phenomenon. The salts and the air which in common with CO_2 are found dissolved in natural water, are indispensable to the duration of the phenomenon. The gas produced contains, in addition to the oxygen, a certain quantity of nitrogen, the result, possibly, of the decomposition of the substance of the plant itself, and which probably the nitrogen of the air dissolved in the water is destined to replace. Ammonia, however, and ammoniacal salts, when dissolved in water, even in minute quantities, hasten rapidly the death of aquatic plants. They only absorb CO_2 by the upper surface of their leaves. The oxygen disengaged in these plants circulates all through the intercellular passages (p. 15)—according to the experiments quoted —"constantly from the leaves to the roots," a fact not supported by Duchartre's observations, he having found it given off by the leaves, as in terrestrial plants. Plants are thus the scavengers of the atmosphere, removing the carbonic acid exhaled by putrefying matter, volcanoes, manufactures, &c., and giving out instead of this gas—so poisonous to animal life—oxygen. Water-plants perform the same office to water—viz., oxygenating it. The amount of CO_2 exhaled at night is small compared with that taken in by the plant during the day.[1]

As carbon, hydrogen, oxygen, and nitrogen—the only four elements absolutely essential as the proper food of plants—all exist in the atmosphere, it follows, from the power of the plant to absorb

---

[1] On the general question of the diffusion of gases in plants, see N. J. C. Müller in Pringsheim's Jahrb., Bd. vi. vii.; Van Tieghen, Ann. des. Sc. Nat., 5e sér., ix. 269 (abstract in Annals of Nat. Hist., 1872, 150); and Barthelémy, Comptes rendus, lxxii.

air and water, that a good deal of the food of the plant may be derived directly from the atmosphere. Some plants, like the "Epiphytes" (various orchids, &c.), derive their nourishment from the air; while others, like some of the Sedums (e.g., *Sedum Telephium*, or "livelong"), can live for a summer with their roots severed from the soil. The plants that germinate on a barren volcanic island raised above the water, or which grew upon the earth for the first time, before the soil had formed by the disintegration of rocks, or the decaying animal or vegetable matter had formed a mould, must have obtained their nutriment from the air alone. In a similar manner a seed which has been grown in powdered flints, and watered with rain-water only, will be found after some time to have increased to fifty or a hundred times its original weight. Plants have been frequently flowered—and even fruited—with no other nourishment than that derived from rain-water, showing that in this fluid were all the necessary nutrient substances.

TRANSPIRATION.

Simultaneously with respiration there is a continuous transpiration of watery fluid going on from the leaves. The cells in the leaf are surrounded by intercellular spaces and canals full of air, so that they may be said to be surrounded by an atmosphere; into these spaces the vapour from the watery contents of the cells passes, from these into the chambers beneath the stomata, from which it escapes either by the mouths of the stomata or by the invisible pores on the surface of the epidermal cells.[1] The result of this evaporation is that the watery sap is thickened, and, combined with the action of the air upon it, is fitted to commence its downward course, and to nourish the plant in its descent. In some cases this water is given off in the form of invisible *vapour*—in other cases, in the form of *drops* which can be easily seen by the naked eye.

Evaporation.—That the amount of watery matter exhaled from leaves in the form of vapour is great, may be gathered from the following statements. Hales found that a sunflower (*Helianthus annuus*) only three and a half feet high, and with 5616 square

---

[1] De Candolle attempted to distinguish the exhalation by the stomata, and that by the invisible pores of the epidermis, which takes place in parts of the leaves where there are no stomata. The first he called *aqueous exhalation*, the second *insensible deperdition*. As both are going on simultaneously, the distinction is scarcely tenable. It is also probable that the air-circulation in the plant changes the composition in different parts of the plant, owing to certain elements being absorbed from it by the sap, according to its requirements.

inches of surface exposed to the air, exhaled at the rate of 20 to 30 ounces avoirdupois every twelve hours — seventeen times more than a man does; a vine with 144 square inches of surface exposed to the air, exhaled in the same period at the rate of five or six ounces; and an apple with 132 square inches exposed, perspired at the rate of nine ounces. Knop found that between the 22d May and 4th September a maize plant exhaled thirty-six times its weight of water. Lawes observed that most of the common agricultural plants—wheat, barley, peas, beans, clover—exhaled during the five months of growth more than 200 times their dry weight of water. Still more extraordinary is the transpiration of the "cornelian cherry" (*Cornus mascula*), which exhales in the course of twenty-four hours water which is equal in weight to twice that of the whole shrub.[1] It has been calculated (by Dresser) that an acre of cabbages, planted in rows 18 inches apart, and 18 inches from each other, would transpire in the course of twelve hours no less than 10 tons, 4 cwt., 3 qrs., and 11 lb. The degree of light, warmth, and dryness of the air also affects the amount of fluid exhaled. The temperature and chemical composition of the soil, and the age and texture of the leaf, have also to be taken into account. If the air is full of moisture, little or none will be exhaled; but if it is in a contrary condition, then much fluid will be given off by the leaves.

The amount exhaled also varies in different species. In an elaborate series of experiments conducted by Dr W. R. M'Nab on the bay laurel (*Prunus Laurocerasus*), the following among other results were obtained. In the leaves of this plant was 63.4 per cent of water; the amount of water which could be removed by the leaves in the sun was 5.8 per cent, though by action of calcium chloride and sulphuric acid about the same quantity could be removed. The rapidity of transpiration in sunlight in one hour was 3.03; in diffused daylight in one hour, 0.59; in darkness in one hour, 0.45 per cent. It was also found that while in a saturated atmosphere *in the sun*, 25.96 per cent of fluid was exhaled in one hour, 20.52 per cent was transpired in a dry atmosphere in the same period. However, when the plant was transferred to a saturated atmosphere *in the shade*, no fluid was transpired in an hour, though in a dry atmosphere 1.69 per cent was given off in the same period. The under surface of the leaf also transpired upwards of twelve times as much as the upper surface.[2] It has been found by various experiments, chiefly by Unger[3] and Sachs, that the amount of water evaporated from a leaf is about from 2½ to 3

---

[1] Duhamel, Phys. des Arbres, i. 145.

[2] See his interesting and valuable paper in Trans. Bot. Soc. Edin., xi. (1871) 45-65.

[3] Anat. u. Phys., s. 333.

times less than would be evaporated from a surface of water of the same space. There is also in each plant a maximum and a minimum of transpiration, the first being about 2 P.M., the second during the night.

This transpiration in leaves acts chiefly through the stomata—transpiration taking place, however, in parts deprived of these, though much more slowly. Garreau and Unger found that the amount of transpiration from the two sides of the leaf was in an exact ratio to the amount of stomata on these surfaces. For instance, the stomata on the upper and lower surfaces of the leaf of Belladona are as 10 to 55, and the quantity of transpiration by the two surfaces is as 48 to 60. In the dahlia, the relative number ot stomata on the two surfaces of the leaf is as 22 to 33, and the amount of water transpired is as 50 to 100,—and so on.[1] The amount of moisture taken up by the root is usually in about exact proportion to the amount of water given off by the leaves, or in the proportion of about 100 to 97.8 ; but, as familiarly seen in warm sultry days, the ratio will be occasionally disturbed—more transpiration than absorption going on—the result of which is, that the plant droops and gets " wilted " looking, and eventually dies, unless the balance is again restored. This transpiration is thus one of the primary causes of the ascent of the sap (p. 249). Evergreens do not " bleed " when cut in the stem in the spring, like the vine, maple, &c., because the continual transpiration going on by their leaves enables them to get clear of their superfluous moisture.

In the air the moisture transpired falls again in rain, after being saturated with the gases deleterious to life, which it washes out of the atmosphere, and again nourishes the plant. Thus it has been calculated that the water raised into the air by evaporation is again condensed, and again evaporated, ten or fifteen times in the course of a year. In a *Wardian case*,[2] which is closed in on all sides, a small amount of moisture suffices—the transpired water being again and again used over, the only consumption occurring being that absorbed into the tissues. It shows the whole economy of vegetable life on a small scale.

Exhalation in the form of drops. — During the night many leaves exude drops of water, which accumulate at the points and serratures. In some cases, these drops are only the insensible evaporation condensed by a fall of the temperature. But it is dubious whether this exhalation is always of the same nature as that just described, and not a true *excretion* of water. Trin-

---

[1] Ann. des Sc. Nat., xiii. (1850) 321-346. See also Barentzy, Bot. Zeitung, Feb. 1872.

[2] Ward, On the Growth of Plants in closely-glazed Cases, 1842.

chinetti[1] has even described little glands (glandulæ periphyllæ) at the spots where the excretion takes place; and the fluid secreted by them, though at first limpid, contains organic substances which pass into fetid decomposition. In a few cases this fluid has an odour resembling that of the plant.

In some of the order *Araceæ* (particularly in *Calla Æthiopica*, *Arum Colocasia*, &c.), water is evacuated in great quantities from the point of the leaves. In *Calladium distillatorum*, the colossal leaves give off each about half a pint each night. In this latter plant, as in *Arum Colocasia*, the water flows from an orifice in the neighbourhood of the point of the leaf, upon the upper surface, in which terminates a canal running along the border of the leaf; while smaller canals, running along the principal nerves, open into this.[2] Even in dry dewless nights, when no moisture is on the surrounding vegetation, there may be noticed drops of water depending from the tips of the branchlets of *Equisetum umbrosum*, (*E. pratense*, Ehr.—one of the "horsetails").

The water secreted in the pitchers of *Nepenthes*, *Sarracenia*, *Cephalotus*, and other pitcher-plants, is most probably of the same nature as the above. That in *Nepenthes* contains only 0.27—0.92 per cent of solid matter, consisting of citric and malic acids, chlorine, potash, soda, lime, and magnesia.[3] The liquid often collected in the flowers of *Coryanthes*, one of the orchids, is clear and somewhat glutinous in appearance, with a specific gravity of 1.062, neutral to test-papers, becoming milky by concentration on the water-bath, and finally yielding a transparent gum insoluble in alcohol. In 100 parts, there are 98.51 of water and volatile oils, and 1.49 of non-volatile residue, thus proving that this liquid is something else than pure water.[4] The water evaporated from the leaves contains also a very small amount of organic matter. It is probable that really no injurious substances are excreted by the leaves by either mode of transpiration; the case quoted in support of the opposite opinion—viz., that the leaves died when the transpiration was prevented by being smeared with oil—being equally capable of being applied in support of the doctrine that death ensued *on account of the leaves being deprived of air* by this means.

It would be wrong, however, to regard even transpiration as a mere physical act, like ordinary evaporation. This is proved (1) by the fact that not only water, but a very minute quantity of

---

[1] Linnea (*fide* Mohl), Bd. xi. s. 66. See also Rainer Graf in Flora, 1840, p. 433.

[2] Mohl, lib. cit., p. 100; Gärtner, Beiblätter zur Flora, 1842, s. i.; Schmidt, Linnea, Bd. vi. s. 65.

[3] Völcker in Ann. of Nat. Hist., 2d ser., i. 178; Phil. Mag., xxxv. 192.

[4] Buckton in Nature, 1870, p. 34.

organic matter, passes off at the same time; (2) that much less water is transpired when the cells are in active health than when their vitality is in any way affected.[1]

CIRCULATION—THE DESCENDING SAP.

The sap has now undergone certain changes in its upward course and in the leaves. From a crude liquid incapable of nourishing the plant,[2] it has become by admixture with the starch, sugar, &c., in the stem, a highly organised fluid, and by evaporation from contact with the atmosphere, thick and con-

---

[1] We have not in the text referred to the observations of M. P. P. Dehérain —not being altogether satisfied with some of his results, or the accuracy of the methods by which they were arrived at. They are, however, too important to be altogether passed over. He proposes to demonstrate the three following points: 1st, The evaporation of water from leaves proceeds under conditions very different from those which determine its evaporation from an inanimate body, for it continues in a saturated atmosphere. 2d, This evaporation is entirely determined by light. 3d, The rays of light which are efficacious for the decomposition of carbonic acid by the leaves are also those which favour evaporation. A leaf of wheat was fixed in an ordinary test-tube by means of a split cork. This tube was exposed at intervals to the action of the sun, and subsequently weighed, when it was found that during each equal period of half an hour the tube (without the wheat-leaf) had increased in weight by almost exactly equal increments, although the air in the tube had become completely saturated, and a considerable quantity of moisture had condensed. Under similar circumstances no increase of weight was found, if, instead of the wheat-leaf, a wick of cotton was inserted in the split cork, one end of which was immersed in water. The quantity of water emitted varies considerably with the species of plant and the age of the leaf; but the most efficacious agent in determining the evaporation is light. In bright sunshine leaves of corn gave off, under long exposure, from 70 to 108 per cent of their own weight of water; in diffused light, from 6 to 18 per cent; in total darkness, from 0.6 to 2.8 per cent, being very little influenced by temperature. Even when the tube was surrounded by ice the leaves gave off an increased quantity of moisture, probably in consequence of the more rapid condensation. Further experiments with coloured solutions showed that the blue or green rays which decompose chloride of silver, but are without action in the reduction of carbonic acid, also do not facilitate evaporation; while the red and yellow rays, which have little photographic power, but have a powerful action in decomposing carbonic acid, have also great influence in promoting evaporation. The series of experiments showed an exact proportion between the quantity of carbonic acid decomposed and the quantity of water evolved. M. Dehérain also confirmed an old observation of Guettard, in 1848, that the upper hard and smooth surface of leaves has more power in decomposing carbonic acid (and hence also in evolving water) than the under surface.—(Comptes rendus, 1869; The Academy, 1869, p. 46.)

[2] This has been repeatedly proved by a variety of experiments. Those who are interested in the matter will find some such described by Hanstein, Wird das Saftsteigen, &c. (Sitzungsberichte, &c., 1864).

centrated. It is now prepared to subserve its function in the vegetable economy by nourishing the plant. To do this, however, it must descend—and descend accordingly it does in a slow stream continuous with the ascending one. The path it takes is through the cellular layer of the bark and the liber, right down to the root, forming—in fact giving birth to—the *cambium* layer, from the inner surface of which the annual layer of young wood is formed, and from the outer surface of which the liber receives its annual increase (p. 89). Apply a ligature very tightly to the stem, and by this means the upward course of the sap through the wood, and the downward course of the elaborated sap through the bark, are demonstrated. Very soon a swelling will form above the ligature, showing that the sap is stopped in its downward course in the *bark;* while no swelling takes place below the ligature, showing that the pathway of the ascending sap is beyond the influence of the ligature—viz., within the wood, not within the bark. This can be even better seen if, instead of a ligature, a ring of the bark be cut out. Then the part of the stem below will cease to increase, and, in the case of the potato-plant, no tubers will be produced; while in the portion above the wound, much thicker layers of wood will be formed, more fruit will be produced, and this fruit will ripen sooner than in ordinary cases: in fact, all the advantages which the whole stem would have derived from the descending stream of nutritive sap will go to that portion above the wound, simply on account of the sap being unable to descend, the bark through which it would have done so being destroyed. This operation of cutting a ring of bark from a tree is known to gardeners as *girdling*, and is taken advantage of to increase the produce, and, as in the case of vines, the size of the fruit produced above the wound. It has also a tendency to cause new (adventitious) roots to be produced—these roots (originating from the vascular tissue) usually springing from the protuberance or *callus*, as it is called, or just above it.

In endogenous plants, the roots, according to Hanstein, are formed for the most part, if not entirely, at the base of the cutting, and not above the girdled place. The same result is seen in some exogens, in which the vascular bundles are not confined to the exterior of the stem, but pass into the pith (e. g., *Piper medium*, *Amaranthus sanguineus*, &c.)

The sap having ascended up to the leaves, from which it is conveyed downward, it may be asked, Is there anything which corresponds to the absorbents, or to the capillaries of the higher animals, found in plants? To this question Mr Herbert Spencer,[1] supported by Dr Pettigrew, has answered in the affirmative. He described, as being found in the leaves, masses of "irregular and

---

[1] Principles of Biology, i. 559.

imperfectly united fibrous cells, such as those out of which the vessels are developed"—forming club-shaped masses, occupying the intercellular spaces between the ultimate venous network of the leaves, into which network they also open. Some of them, however, open outwards towards the air. "They are also found in the root and body of the turnip, in the simpler form of fenestrated cells, with their ends bent round so as to meet. If this is so, then there is direct communication between these club-shaped masses and the vascular tubes found in the stems, branches, and roots—in fact, a system of absorbents and capillaries in one." Pettigrew therefore considers that the circulation goes on in the form of a set of siphons. Without, however, denying that such a system of absorbents does exist, we must warn the student that this doctrine is not generally held, and that we are not aware of any botanist who has yet been able to see these absorbents; after repeated efforts, we have failed to demonstrate them. Moreover, they are not found, according to Mr Spencer, in all leaves, though in many stems, &c., taking on the function of leaves.

At all events, whether we believe in this or not—and the temptations to do so are captivating—there can be little doubt that the sap descends after being elaborated in the leaf; and the next question is, *Does the descending sap travel in any definite canals, or simply by endosmose or exosmose?* To this question we may answer that it is now generally believed that there are certain definite conducting tissues in or about the bark through which it descends. These are: 1. The *Cellulæ clathratæ*, or "cribriform cells or tubes"—the *vasa propria* of v. Mohl—which we have already described (p. 43). They form a system which accompanies the fibro-vascular bundles in every part of the plant; and in the liber their existence is even more general than the laticiferous vessels, and even the liberian fibres themselves. 2. Nägli has described as lying outside of the cambium, and very like in form to the cells of that layer, but altogether distinct from it, a series of thin-walled delicate cells, which he has called the *cribriform cells*. 3. The *cellulæ conductrices* of Caspary (p. 13), which are an essential element of most of the woody bundles, and contain mucilaginous or albuminoid contents, and often replace the cribriform tubes, are believed to assist in conveying the descending sap. These different tissues, owing to their thin walls, or, as in the case of the cribriform cells (or tubes), the openings in the walls, are peculiarly suited for conveying the sap downward, and distributing it to the cambium. The contents of all these vessels or cells named are alike in this respect, that they are rich in nitrogenous materials—more or less mucilaginous, and very thick. Hanstein's researches have left little doubt that their function is the conveyance of this nutritive sap, though Schacht has taken exception even to the expression "descending sap"—considering that it is simply an exchange of sap between the different cells by means of endosmose; a view which it would be about equally difficult to prove or disprove.

Notwithstanding the various experiments detailed above, the descent of the sap through the bark has been denied by Herbert Spencer, who considers that its course is through the young wood—an idea not remarkable for its intelligibility.[1] Schleiden (and others both before and after him) has even denied—and what is still more singular, attempted to support his denial by proof—that the sap descends at all, explaining the increased growth above the "girdling" by an artificial interruption of the upward current of crude sap, "in consequence of which the sap contained in the upper part of the plant must soon become greatly concentrated and potential for development."[2] To such an idea the best reply is the characteristically sarcastic but not less unanswerable one given him by Hugo v. Mohl: "When we can succeed in fattening an animal by depriving it of a portion of its accustomed food, this explanation may be received as satisfactory."

Notwithstanding the crotchets of the botanists referred to—Dupetit-Thouars, Turpin, Schleiden, Hérincq, &c., who, to support some theories of their own, have either denied the circulation of the sap *in toto* or partially—there can be but little doubt that few facts are better established in vegetable physiology than that the sap ascends from the root to the leaves, and again descends in an elaborated condition from the leaves towards the root. There may be occasional exceptions, as in cereals, when the plants, as they approach maturity, lose the power of elaborating nutriment by their leaves—the flowers, &c., subsisting by the nutriment stored up in the stem; or as in the case of biennial root crops, when in the first year the nourishment is stored in the root, and in the second rises *upwards* to nourish the plant. That the elaborated sap also sometimes ascends is proved by the fact that "undeveloped buds perish in most cases where the stem is girdled between them and the active leaves." In these exceptions the vascular bundles, as in the instances previously mentioned, pass into the pith. Still the broad fact remains the same, that though nutriment can be transferred by means of the sap to whatever part of the plant requires it, yet the general course of the sap is upwards and downwards.

---

[1] Principles of Biology, i. 550.

[2] Grundzüge, &c., Auf. 2, Bd. ii. 513.

SECRETIONS AND EXCRETIONS.

It may be asked, Does not the elaborated sap, in the process of forming the substances necessary for the nutrition of the plant, also form some substances which are not necessary for nutrition, or are even injurious to it, and which, therefore, must be excreted from the organism? After the descending current has reached the root, is there no refuse; and if there is, where does this refuse go to?—is it absorbed in the sap of next year, or thrown out of the plant altogether? This idea has been held, and is yet to a small extent maintained, by some botanists, and by the majority of agriculturists, though, as we have already hinted, on very feeble grounds.

Root-excretions.—It has been pointed out, in support of the excreting power of plants, that there frequently appear on the surface of roots substances which swell up in water, and which enable the particles of earth to cling to them. It has also been pointed out that certain plants do not prosper in the vicinity of others—in a word, that these plants have "antipathies" to others. This subject we have already mentioned casually when describing the functions of the root (p. 141); and as it is one which has excited no little controversy, we may devote a few more paragraphs to it in this place. By the advocates of these antipathies of certain plants it was believed that particular plants emitted certain fluids or other substances from their roots, which corroded, or in some way poisoned, the roots of particular species growing in their vicinity. The idea was long entertained, chiefly through agriculturists observing that particular crops would not prosper in ground which had been occupied by others, and *vice versâ;* or that certain plants would not prosper if growing side by side. It is owing to the observations of Macaire-Prinseps,[1] undertaken at the instigation of De Candolle, that this idea has taken ground among vegetable physiologists. He seemed to have found, by the most positive experiments, that certain plants gave off chiefly during the night certain substances, different in each case according to the kind of plant examined. For instance, in *Lactuceæ* (lettuces) and the poppies the excretion was opium-like, that from *Euphorbiæ* (spurges) acrid, that from *Leguminosæ* (bean and pea order) mucilaginous, &c.; and that even if the plant was made to imbibe certain substances foreign to it, these substances would be afterwards rejected. Finally, he considered it proved that while some plants would prosper in the water (or soil) into which these excretions had passed, others would not grow at all. From these experiments De Candolle and his followers drew the conclusion that these root-excretions were analogous to

---

[1] Mém. de la Soc. de Phys. et d'Hist. Nat. de Genève, v. 282-302.

the urinary excretions of animals; and that as animals cannot live upon their own excretions, so neither could plants. Hence cereals could not be long uninterruptedly cultivated in the same soil. However, subsequent experiments undertaken by other physiologists[1] showed either a perfectly negative result, or that Macaire-Prinseps had proceeded without much circumspection—only wounded or irritated roots yielding anything in the shape of excretions. It would be tedious, even if space permitted, to go into these experiments in detail. Suffice it that this is the result arrived at, and that at best the question of root-excretion is *not proven.* The true theory of rotation of crops, as already mentioned (p. 141), lies in the selective power of roots, and in the fact that certain crops can grow on soil after others, owing to the different media they extract certain essential nutritive substances from. For instance, leguminous plants (like beans, peas, tares, &c.), prosper after cereals (wheat, barley, oats, &c.), from the fact that the first order of plants derive their nitrogen from the air, and the other from the earth; the one *exhausts*, the other *improves* the soil. While denying the power of the roots to secrete (and excrete) substances either beneficial or prejudicial to other plants, we cannot shut our eyes to the fact that roots exert chemical influences on certain hard bodies which it is difficult to see are not produced by some excreted substance. Gazzeni, according to v. Mohl, saw this in clover, and Trinchinetti[2] saw a root of *Nepeta Cataria* grow through the midst of a peach-stone. Moreover, Trinchinetti observed that a decoction of humus underwent fetid putrefaction when left to itself; but when the roots of living plants were placed in it, this did not take place. Gardeners have noticed that the debris of horn gets consumed much more slowly in earth not covered with vegetation than in similar ground in which grow plants, the roots of which penetrate in every direction (Martins). It is also probably owing to the secretion of a free acid that the roots of *Colocasia antiquorum* have the property of keeping water from putrefaction. Schacht, indeed, informs us, that in Madeira even the petioles of this plant put into water will keep it sweet for some days. This is probably done by means of the excretion of a free acid—most likely acetic—"or of a substance which is converted into an acid in the air." Becquerel even goes so far as to declare that there is a free acid excreted from not only the roots, but from the bulbs, tubers, buds, and leaves. The roots of some plants seem to have a corroding influence on marble (as proved by numerous observers, and more recently by Sachs), and lichens will dissolve the limestone they

---

[1] See Bracconet, Ann. de Chim. et de Phys., lxxxii. 27; also Meyer's Jahresbericht, &c., 1839, s. 5.

[2] Sulla facoltà assorbente delle radici, 57.

grow upon, all of which points to the secretion of an acid of some kind, unless, indeed, this is owing to the CO_2 dissolved in the water. Of the numerous hypotheses which have been framed on this subject, the student had better remain ignorant, since these are entirely unsupported by aught but the vivid imaginations of their manufacturers—*voces et præterea nihil.*

Leaf-excretions.—There are, however, certain excretions in the plant, though not given off by the root, but chiefly by the leaves and the epidermis generally. Of this nature we are inclined to regard the resinous substance seen on the buds of many plants, the sugary substances which cover the sycamore-leaves in the course of summer, the fragrant resinous substance covering the leaves of *Ceanothus velutinus* (the Cinnamon laurel) of North-West America, the saccharine excretion of orange-trees, the gummy matter on *Lychnis Viscaria*, &c., the resins of firs, pines, and other Coniferæ, the sugar (*pinite*, p. 215) given out from the bark of the sugar-pine (*Pinus Lambertiana*), the wax of the leaves and stems of the candleberry myrtle (*Myrica cerifera*), and the layer of wax which covers the wax-palm (*Ceroxylon andicola*), and probably flows from the base of the leaves. Of a similar nature are probably the excretions given out by the hair-like structures on the leaves of *Drosera* (p. 61), and the acrid substance on the hairs of the chick-pea (*Cicer arietinum*), the gummy secretions of Primulaceæ, Sileneæ, &c.—these last being found only on particular plants, and serving special and not general purposes.[1]

The gyration of the contents of the interior of many cells (p. 20), and the cyclosis observed in the milk-vessels (p. 44), are also minor local circulations, each being a sort of *imperium in imperio.* Nothing of the nature of a true or general nourishing fluid can, however, be supplied by the latex of the milk-vessels, as supposed by some physiologists (De Candolle, Schultz, &c.), who have even

---

[1] On the subject of excretions the student is referred to the following works, in addition to those already quoted : Duhamel, Physique des arbres, i. 86-87 ; Brugman's De mutata humorum in regno organico indole (1789) ; Plenk, Physiologie ; Humboldt, Aphorism a. d. chemisch Physiologie der Pflanzen, 116 ; Cotta, Naturbet. über Bewegung d. safts ; Boussingault, Ann. de Chim. et Phys., 1841, 217 ; Unger, Über d. Veget. v. Kitzbühel, s. 149 ; Meyen, Physiol., ii. s. 530 ; Guillemin, Archiv. de Botanique, i. 398 ; Moldenhawer, Beiträge zur Anat. der Pflanzen 320 ; Gyde, Trans. Highland and Agr. Soc., 1845-47 ; Schleiden, lib. cit. ; Schultz, Die Entdeckung der Wahren Pflanzennahrung ; Mohl, Vegetabilische Zelle, and trans. by Henfrey ; Chatin, Comptes rendus, xx. (1845) 21 - 29, &c. ; Roche, De l'action de quelques composés du règne minéral sur les végétaux ; Cauvet, Etudes sur le rôle des racines dans l'absorption et l'excrétion, 1861 ; Sachs, Handbuch, &c. ; Bracconet, Ann. de Phys. et Chem. (1839), lxxii. ; Unger, Ann. des Sc. Nat., viii. (1838) ; Meyen, Neues System d. Pflanzen Phys., ii. s. 529 ; Walser, Untersuch. über die Wurzel Ausscheidung, 1838, &c.

been inclined to look upon it as the descending sap. Did the latex serve so important a purpose, we might be certain that it would be much more universally distributed throughout the vegetable kingdom. On the contrary, it is only found in a few orders, and has not even the same properties in all, being poisonous in some, nourishing or innocuous in others. Trecul[1] looked upon it as a deoxidised fluid, analogous to the venous blood, which in passing into the vessels proper gets oxidised like the arterial blood. Hence he called the laticiferous vessels *venous*, and the vessels proper *arterial* vessels. It is, however, just possible, from the researches of Hanstein and Favre, that in the plants in which the latex is found it may serve some minor purpose in nutrition. There is, however, no doubt but that it is not a true or universal nourishing fluid which is organisable, the elaboration of that being confined, as we have seen, to the leaves. We are not, however, authorised, in the present state of our knowledge, to coincide with the ingenious theory of Sachs, that there are in plants two nutritive fluids,—one rich in nitrogenous materials which supplies the cambium; and the other which forms the non-nitrogenous materials such as starch, inuline, sugar, &c., traversing as its pathway the bark, the pith, the periphery of the tubers and the parenchyma generally. Without going into details, we may see that this idea is contrary to some primary facts, and is held by but few botanists.

ASSIMILATION.

The sap has ascended to the leaves; there it has been elaborated; and finally the sap, so elaborated, has descended in a condition fit for the nutrition of the plant, the result of which is the growth of the tissues. Here, again, we are brought face to face with one of the most important, but at the same time most difficult, problems in all vegetable physiology. At the very outset it seems difficult to imagine how materials all soluble in water, as the primary nutritive substances of the plant must be, can form substances like lignine, &c., perfectly insoluble in the same liquid; and finally, how all the varied substances—oils, acids, salts, &c.—found within the cells, can be formed from the same set of materials. We see that there is one point of agreement in all plants—viz., that all produce a series of neutral hydrates of carbon, out of which all the solid materials of plants are formed, and also the proteine substances which take so active a part in cell-development. We can easily see that all these materials are formed by some series of chemical changes within the plant; by the reaction of various of these substances—either in their

---

[1] Ann. des Sc. Nat., 1857, vii. 288-301.

primary or secondary states—on one another: the result of which combinations we see in the cell-wall's incrustations and the cell-contents. For instance, cellulose, out of which the walls of the cells—the ultimate microscopic elements of all the tissues—are composed, in chemical composition is C, H, and O; in other words, it consists of carbon and the elements of water. If, then, the CO_2 taken in by the leaves is decomposed, carbon and the water (H and O) taken in by the roots remain; so that we have thus the exact elements of cellulose supplied to us. We can see that every facility for these chemical reactions is found in the ever changing and interchanging of the cell-contents by means of exosmose and endosmose; for if this law is true, they can never be for one moment at a stand-still: even were the plant filled with a liquid of uniform consistency, in a short time evaporation at some particular part would determine the commencement of endosmose and exosmose. As Mohl has pertinently observed, remarkable changes must occur in cells like those, for instance, of the leaves which have ammonia derived from the soil on one side of them in the ascending sap, and CO_2 derived from the atmosphere on the other. We can see—as Richard has pointed out—that three processes at least are concerned in forming the substances which the plant is composed of—viz., (1) a *chemical* action, by which the primitive elements of the plant—C, O, H, and N—are isolated and absorbed by it; (2) an *organic* or *physiological* action, by which the elements combine to form immediate principles; and (3) a *physical* action, through which inorganic materials (metals, alkalies, sulphur, silex, &c.) which are found in the ash of plants are allowed to penetrate into the plant and form a component portion of it.

Summing up our knowledge of the distribution of these substances in the tissue, it may be said that (1) the cambium and the tissue which are formed from it are rich in nitrogenous principles; (2) the parenchymatous tissues contain about all combinations of carbon and hydrogen, and their contents are starch, inuline, dextrine, and sugar, resins, oils, colouring materials, organic acids, crystallised salts, &c.—the cortical cells secrete alkaloids (strychnine, morphia, quinine, &c.) and caoutchouc; (4) indurated cells —*i.e.*, those thickened by internal deposits—contain air, lignine itself being a product derived from cellulose; (5) combinations are not formed in the epidermis in general; (6) cork, which does not long remain in a living state, is equally derived from cellulose. One parenchymatous cell labours for the benefit of another; hence, as we shall see by-and-by, the little cells of the anthers prepare the substance which is in due course utilised by the larger cells, which generate the pollen-grains. The endosperm furnishes the necessary nourishment which the embryo requires. The cotyledons in their turn do the same good office for the young plant before it has taken root in the ground and can nourish itself from the soil. The parenchymatous cells which surround the reservoirs of resin transform starch into a substance which gets brown under the action of iodine; this again is changed into essential oil, which in its turn becomes resin (Schacht).

Yet after all, we are not one whit nearer the question of how each of them, or out of what materials each of them, is formed. In the secret recesses of the plant are chemical processes going on that we cannot do more than guess at. We know such must be going on, and in some cases we can reasonably enough pretend to say what they must have been from seeing the result; yet until we know how and in what stage and quantity each substance is brought into contact with the others, we are only vaguely groping our way in a thicket of conflicting hypotheses. Some of these processes the chemist may be able to demonstrate in his laboratory; but still chemistry will not enable us to explain all—for light, shade, and other imponderable physical agents, have their share in regulating these processes; and above all, the vital principle which takes no share in the mere operations of the laboratory presides over those within the living plant. Indeed, in all the questions of assimilation, of only one thing can we be certain, and that is, that carbon and water remain in the plant, and are applied to the building up of its structure. Even that it is by the decomposition of CO_2 that O is given off is by no means perfectly certain. For has not Mülder, an eminent Dutch chemist, even broached the opinion that O is set free from the decomposition of an organic substance previously formed, and that the plant does not decompose CO_2 because of its chlorophyll, but while the chlorophyll is forming? Draper has even doubts whether nitrogen is not also given off, though it is now very generally admitted, as we have taught, that O is given off under sunlight; but again, in addition to the hypotheses given, there is another—that it may be due to the decomposition of water. Again, we are not one degree surer as to what combinations the absorbed nutriment first enters into. At every step we meet with difficulties insolvable in the present state of our knowledge. The process of assimilation is a threefold one—chemical, physical, and physiological—and is much too complicated for us, with our present means of research, to follow. Everywhere we are met by abundant crops of hypotheses, without any facts to support them, and with theories in the presence of which facts fare but indifferently. Assimilation is essentially a question of organic chemistry, and there the botanist is glad to leave it. In a word, the author would best perform his duty to his readers if, following the example of his distinguished teacher, M. Duchartre—he at once informed them that so little is known about assimilation, and that little so imperfectly, that the limited space of a student's text-book is better occupied with matters regarding which we can speak more confidently and satisfactorily.

THE INCREASE OF THE PLANT.

In whatever way the ultimate materials out of which the organs are formed are derived from the descending fluid, the invariable result is the nutrition of the plant, and the consequent increase of its bulk by the increase of the individual organs composing it. The nutrition of the plant is a twofold act. It consists, firstly, in keeping up the organs in their integrity; and secondly, in increasing these, and thereby the whole plant.

The way this is done is best seen in the stem of Dicotyledons. Here, as we have already seen, the stem is annually increased by layer after layer of wood being laid down, one over another, around the pith as the central object. If we examine the stem during the winter, we will find between the bark and the wood a cellular layer without green matter in it. This layer we already know as the *cambium*. In summer, when the sap descends, this gets gorged with the nutritive fluid, and at this time it is easy to separate the bark from the wood. The cells of this cambium are regular in shape, with thin transparent walls. If the bark is raised and the cambium rubbed off, no new wood is formed. However, if nothing interferes with its natural growth, insensibly in the progress of growth some of these cells are elongated, their walls become thicker, and they then present the character of fibrous tissue. About the same time, a certain number of the cells scattered in the midst of the former augment in diameter and in length; the thin walls show transparent punctations, either in the form of transverse lines or in scattered "dots," and thus get converted into barred and punctated vessels (p. 49). These form bundles united by cells, and so form a layer of woody matter exactly the same as the one before it, which it covers over. Some of the outer vessels branch and form a new coat of liber, thus giving the increase to the bark. All the newly-formed fibres and vessels take the same character as those over which they are superimposed. For instance, if cells are in contact with dotted cells they become dotted—if in contact with barred ones they have similar transverse markings,—and so on. Hence Duhamel said that "vessels produced vessels, and cells produced cells." The rest of the process has been described in describing the development of the stem (p. 80). This is the increase in *diameter*. There is, however, another increase, to which attention was first called by Link and Dutrochet, and which they styled the *lateral* increase. Like the first, it contributes to the increase of the thickness of the stem, but in a different way. After the vascular bundles have once formed, either in the bark or the wood, they have a tendency to divide into two by the formation of cellular tissue in their middle ; these two again into four,—and so on by the same means until at the end of the year perhaps twelve woody bundles will be found at the base of the same; next year there may be twenty-four,—and so on. Now all this contributes to increase the diameter of the stem by pushing out laterally as it were—quite different in character, though in final result the same, from increasing the thickness by the formation of layers of superimposed wood.

The *increase in height* of the dicotyledonous stem has been already described (p. 76) as being effected by the growth of the terminal bud, which in the newly-germinated plant is the *plumule.* This is composed of an axis and of rudimentary leaves. As the axis elongates, the leaves expand and gradually take the characters they are destined to assume. At each "node" the year's growth terminates with the terminal bud, which is next year in a similar manner to carry on the growth. At the same time, it increases in diameter in the manner already described—each year a new coat of wood covering that formed the year before. The axis is therefore a series of very elongated cones, composed of the woody layers placed one upon the other. The summit of the innermost cone is arrested at the base of the second node or year's growth, that of the second at the third, and so on in succession with the others. It is then at the base of the trunk that the number of woody layers corresponds to the number of years of the plant. Thus, for example, a stem ten years old shows at the base ten woody layers, at commencement of second year's growth nine, eight at the third, and so on until there is only one at the summit. It is owing to this that the trunks of Dicotyledons are somewhat conical—in a word, "the number of woody layers being gradually more in number as we get from the summit to the base" (Richard). In *endogenous stems* we are not so well acquainted with the course the sap takes; but it probably ascends and descends in the isolated woody bundles, the cellular tissue also taking part in this function. Their increase we have already described (p. 95). In *acrogenous stems* the course of the sap is most likely also in the woody bundles. In herbaceous Dicotyledons, in which the woody bundles often remain separate, the course is similar. In ferns, Hoffmann considered there were no channels for the descent of the sap—the fluid simply ascending and diffusing itself through the substance of the plant in its progress.[1] Finally, it might be remarked that though we are enabled to see the cambium best in exogenous stems, it is also found in *endogenous* and *acrogenous* ones; in the former, in the interior of

---

[1] Taylor's Scientific Memoirs, vol. i.

the woody bundles—and in acrogens, round them. In these stems, however, the cambium soon lignifies, and the increase is probably carried on at the upper ends of the bundles by means of unhardened cambium cells. We are, however, still much in the dark in regard to these questions.

In Monocotyledons there is, in the vast majority of cases—especially in those with woody stems—only a terminal bud which carries on the growth. If this is destroyed the plant dies. However, in a few cases, as in the screw-pine, &c., lateral buds are developed, and from them spring branches.

Now we see that this assumed method of increasing the plant by producing the annual layer of new wood is exactly in accordance with what we have already been taught regarding the growth of cellular tissue, and is in all likelihood the right one. Du Petit-Thouar's (or rather Lahire's) theory[1] of the young wood being merely the roots of the bud, which he looked upon as a young plant rooted in the stem, is so entirely erroneous that it is abandoned by nearly all scientific botanists; and ranking as it does among the other abandoned theories of the production of new wood, need, in common with its companions in misfortune, have no further space wasted on it.[2]

To trace the growth of new tissue is much more difficult than most other researches in vegetable anatomy or physiology, where we can have the object under examination under our own eyes. Here all is concealed, and great care is requisite to avoid errors, as the numerous futile attempts of former operators have abundantly proved.

A curious fact mentioned by Dutrochet would at first sight seem to militate against the *rationale* of nutrition as explained in the foregoing pages. A number of stumps of firs (*Abies pectinata* and *A. excelsa* chiefly) which were cut down within a few feet of the ground, produced annually each a new though very thin layer of wood, without the intervention of any leaves on the stump to elaborate the ascending sap. In reality, however, this was not so; for on closer examination it was found that the roots of these stumps were ingrafted on the roots of some trees of the same species growing in the immediate vicinity, the result of which was, that the leaves of these trees in all likelihood supplied the elaborated sap out of which the annual layers of wood were formed on the leafless stumps.[3]

---

[1] Adopted and extended by Goethe, Gaudichaud, Trecul, and others.

[2] This *vertical* theory of the formation of wood, as, in contradistinction to the *horizontal* theory adopted in these pages, it has been called, is supposed to account for the growth of plants in an upward direction, and by the presence in some pines of adventitious roots which descend into the soil.

[3] Similar facts have been stated several times since. For instance, at the

Finally, before leaving this subject we may point out an essential difference between the nutrition of plants and that of animals. In animals, every particle of the structure is in course of time renewed by interstitial nutrition; while in the plant, the parts, once formed, are never renewed in this manner, but either die and fall, to be replaced by similar organs next year, or remain unchanged, cease to be nourished, and therefore soon lose their vitality, while new parts are continually found to take their place—these in their turn to be replaced by others.

Whether the plant increases at a greater rate during the day or night has long been a subject of controversy,[1] and is still *sub judice*. The latest researches on the subject are those of a Dutch botanist, Dr W. P. Rauwenhoff, made chiefly on *Bryonia dioica*, *Wistaria Chinensis*, *Vitis orientalis*, *Cucurbita Pepo*, and *Dasylirium acrotrichum*. He found, as a general result of his observations, that (1) the stem increases most during the day, less by night; (2) that, however, during certain periods the nocturnal increase is greater—and as this is found in plants of very different natures and developments, it indicates some general action the nature of which is not precisely known; (3) the elongation of the plant is quicker in the afternoon than in the morning, though at certain intervals the opposite is true (*e.g.*, in *Cucurbita*, from 10th June to 10th July), yet as a *general* course the increase in length is greater in the afternoon; (4) the ratio of increase differs in different species; and (5) it usually corresponds to an increase or diminution of temperature, being greater when the temperature is higher, and *vice versâ*—as might have been presaged from what we know of the effect of the same agent on the flow of the sap.[2]

---

meeting of the Scottish Arboricultural Society in 1873, Messrs Robertson and Sadler exhibited a stump of a larch-tree which had been felled about thirty years ago. The stump had continued ever since to increase by additions of wood to the outside, while the central part had decayed. It was found, on tracing the roots proceeding from the stump, that some of them had got ingrafted into the roots of another larch growing about three feet distant.

[1] Ventenat, Bulletin de la Soc. Philom., 1795; Meyer, Verhand. des Vereins zur Befurdnung des Gartenbaues in den Preussischen Staaten, 1828; Meyer, Linnea, 1829; Munter, Bot. Zeit., 1843; Mülder, Bijdragen tot de Natuurkunde Wetenschappen, iv. 1829; De Vriese in Van der Hoven, and De Vrieses Tijdschrift van nat. geschiedenis en Physiologie, iii. 1836; and in Nederlandsch Kruidkundig Archief, iii.; Hartig, Tijdschrift, ix. 1842; Karsten, Bot. Untersuch., 2d part, 1866; and Martin and Quételet in various papers.

[2] Verslaegenen Medeelinger der K. Akad. Van Wetenschaffen (2d ser., Sect. of Nat. Sc.), ii. 134-161 (1869).

SECTION III.

REPRODUCTION

CHAPTER I.

GENERAL REMARKS ON THE FLOWER AND FLOWERING.

"THE fructification is," in the words of Linnæus,[1] "a temporary part of a vegetable destined for the reproduction of the species, terminating the old individual, and beginning the new." The aim and end of a vegetable existence is to produce flowers, and from them and by them fruit and seed, so as to continue and reproduce the species. To use the language of the famous Roman naturalist, "Blossoms are the joy of trees, in bearing which they assume a new aspect, vying with each other in luxuriance and variety of colours."

The part of a plant concerned in reproduction is the *flower*, which, in a perfect state—*i. e.*, when possessing all its normal parts,—consists of (enumerating from without inwards), 1. the *calyx*, composed of the *sepals;* 2. the *corolla*, composed of the *petals;* 3. the *stamens*, each composed of *filament* and *anther;* 4. the *pistil*, of one or more *carpels*, *styles*, and *stigmas*,—the whole supported on the termination of the *peduncle* or flower-stalk, which corresponds to

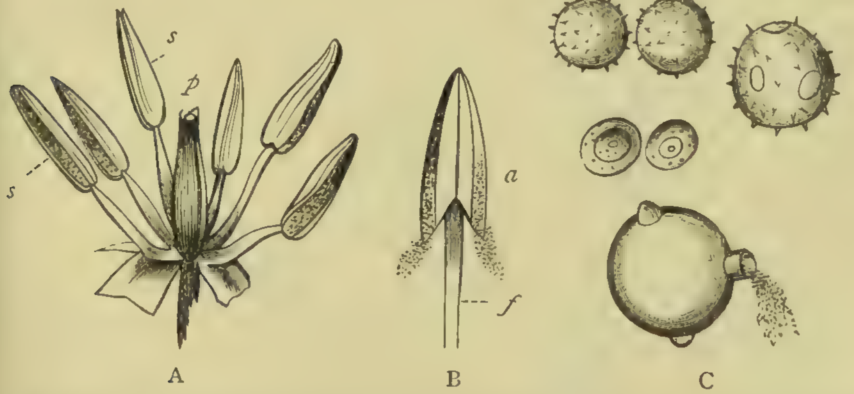


Fig. 139.—A, Flower of Tulip with the external parts removed, showing the six stamens (*s*) surrounding the pistil (*p*). B, Single stamen enlarged, showing anther (*a*) and the filament or stalk (*f*). C, Pollen-grains enlarged, one of them discharging the fovilla.

---

[1] Phil. Bot., 52.

the petiole of the leaf (figs. 139, 140). The calyx and corolla are, however, often wanting, singly or both—the only parts of the flower essential to the production of fruit and seed being the stamens and pistils; and even these may not be found on one plant, or in each flower on a particular individual plant. It may happen that the stamens are alone found on flowers on one part of a plant, while the pistil is alone found on the flowers on another part; or quite as commonly the whole of the flowers of one individual plant of a species may have only *staminate* flowers, while another may have only *pistillate* flowers: in other words, one having only stamens, the other only pistils. As the union of both organs is necessary to the production of seed, the contact of the essential portions is accomplished by means which we will explain when considering the physiology of reproduction. The calyx or outer covering, and the corolla or inner one (generally bright-coloured), are not essential, and are often entirely wanting. But no seed can be produced without the aid of the stamens and pistils. The seed produced, the functions of the plant have ended, so far as its aim of life is concerned; the seed falls into the ground, or other medium in which it is to vegetate; it germinates, grows up, produces leaves, then flowers; then this flower performs certain functions, necessary to fertilise certain parts within the flower which produce the fruit—the fruit containing the seed—this seed again reproducing and continuing the species; and so the cycle of life goes on. All the other functions of the plant are only subservient to reproduction. After the flower

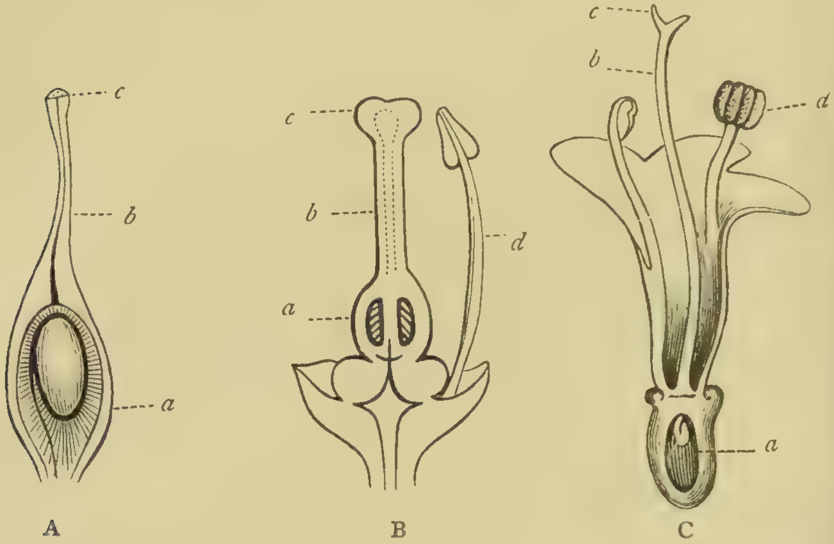


Fig. 140.—A, Pistil of the Apricot. B, Pistil of the Orange. C, Flower of Valerian, cut vertically. *a* Ovary, containing the ovule or ovules; *b* Style; *c* Stigma; *d* Stamen.

has arrived at that stage at which it may produce seed, the subsidiary corolla fades, while the lower portion of the pistil swells and becomes the fruit, contained in which are the seeds.

We have said that all the above-named parts of the flower may not be present in every flower, and have instanced cases of variation. If all the essential parts—viz., the stamens and pistils—are present, then the flower is said to be *hermaphrodite;* if only stamens or pistils, it is *unisexual*—the terms *staminate* and *pistillate* being applied to the particular kind of organs, stamens or pistils, found in such unisexual flowers. Again, a plant is said to be (1) *monœcious*[1] when the stamens are on one flower and the pistils on another flower of the same individual plant. Such a plant is the maize or Indian corn (*Zea Mays*), where the staminate flowers or "tassels," as they are commonly known to the farmer, are at the summit of the stalk, while the pistillate flowers or "silk" are lower down. The hop, and various species of *Carex* (fig. 141),

Fig. 141.—Flowering plant of *Carex arenaria* (*c*). *a* Female flower; *b* Male flower.

---

[1] μόνος, one; οἶκος, habitation.

also afford examples of monœcious plants. Again (2), *diœcious*[1] plants are those in which the stamens are on one individual plant and the pistils on another (*Ex.*, hemp (*Cannabis sativa*), *Aucuba Japonica*, &c.); (3) *polygamous*[2] flowers, in which the same species may have staminate and pistillate or hermaphrodite flowers on each plant, or on two or even three different plants. In various species of *Viburnum*, *Hydrangea*, and even in certain monstrous states of the whole cluster, owing to cultivation, as in the garden guelder rose (*Viburnum Opulus*), Gray has shown that in the blossoms occupying the margin of the cyme both the stamens and pistils may be wanting. Such flowers are called *neutral*, being neither staminate nor pistillate. It occasionally happens, also, that the marginal or *ligulate* flowers of some of the "composite" flowers (*e.g.*), *Coreopsis*, may-weed (*Maruta*), and sunflower, may be neutral. Hemaphrodite flowers are the more common of the category, the rarity of the other kinds being in an inverse ratio to the order in which we have mentioned them. Various signs are used by descriptive botanists to express the character of a flower in the above respects. The following are the principal ones used: for staminate flowers, the astronomical sign of the planet Mars ♂ or ♁ (the sign of the earth); for pistillate ones, the sign of the planet Venus ♀; while for hermaphrodite flowers the two signs are united as follows, ⚥

The following synopsis gives a *précis* of the conditions we have mentioned, with a few minor terms:—

A.

COMPLETE FLOWERS [in four verticils].

- I. **Floral Envelopes (perianth or perigone).**
  - 1. *Calyx*, 1st verticil composed of *Sepals.*
  - 2. *Corolla*, 2d verticil composed of *Petals.*
- II. **Sexual or Reproductory Organs.**
  - α. Considered in reference to *themselves.*
    - 1. *Andrœcium.* 3d verticil formed of *Stamens.* [Also of filament, anther, and pollen.]
    - 2. *Gynœcium* (pistil), 4th verticil formed of *Carpels.* [Also of ovary, ovules, style, and stigma.]
  - β. Considered in reference to *their functions.* The inflorescence being in one flower, renders this flower *Hermaphrodite.*

B.

INCOMPLETE FLOWERS.

- I. **Those wanting the Perianth.**
  - 1. Wanting the corolla, the flowers are *Apetalous* (monoperianthous or monochlamydeous).
  - 2. ,, both calyx and corolla ,, *Naked.*

---

[1] δύο, two; οἶκος, habitation.

[2] πολὺς, many; and γαμέω, I marry.

II. As concerns the Sexual Organs.

1. When the stamen is alone present the flowers are *Staminate or male.*
2. ,, pistils are ,, ,, *Pistillate or female.*
3. When there are staminate and pistillate flowers on the same plant the flowers are *Monœcious.*
4. When there are staminate and pistillate flowers on different plants *Diœcious.*
5. When unisexual and hermaphrodite flowers are on the same plant, the inflorescence of the plant is said to be *Polygamous.*
6. When the stamens and pistils are entirely wanting *Neutral.*

Flowers generally grow from the axils of little leaves called *bracts*, and though they are generally at the end of peduncles, when they are called *pedunculated*, yet this flower-stalk may be wanting; in this case the flower is styled *sessile*. This peduncle is apparently a branch, at the summit of which the parts which it supports are united in the form of appendages to the axis, which is their support. This summit, to which they are all attached, and which is usually more or less expanded, is called the *receptacle*, *torus*, or *thalamus*.

The calyx, corolla, stamens, and pistils are, notwithstanding their varied forms and functions, only modifications of one another, and all are, again, only modified leaves. So that not only in the arrangement of the parts of the flower, but in their character also, the organs of reproduction are modifications, for a particular purpose, of those of nutrition. The flower is in reality terminated by a bud and shortened branch, the axis of which is not elongated further, but has its leaves (viz., the sepals of the calyx, the petals of the corolla, and the stamens and pistils) arranged in the form of a rosette, like what we see in the leaves of many plants—*e. g.*, the house-leek. The four circles of the parts of the flower appear to be simply verticils, like the verticils of leaves. Yet when we carefully examine the arrangement of the floral organs, we will find that, like the leaves, they are arranged in a spiral, closely crowded together, but nevertheless, with the component members of the verticils, plainly alternating one with another. To this law of the alternation of the sepals of the calyx with the petals of the corolla, and these again alternating with the stamens, and the stamens with the pistil or divisions of the pistil, there are very few exceptions. Such an exception might seem to be found in the tulip, where there are six stamens *opposite* the six faces of the segments of the "perianth," or gay-coloured, corolla-looking, outer covering. This is not, however, really the case; for in this plant, and indeed in most monocotyledonous "flowers," the calyx is alone present, the place of the corolla in the tulip, for instance, being supplied by the gaudy-coloured calyx. However, some botanists take another view, and say that in monocotyledonous plants there are both calyx and corolla present, but that the calyx consists of three sepals, the corolla of three petals, and that the andrœcium or staminal whorl is in reality also in two verticils, each of three stamens. Hence in this manner it is explained how in such plants we find the stamens opposite to instead of alternating with the segments of the whorl of floral organs next to them. In the great division of dicotyledons, again, instead of having the floral organs in three, or multiples of three, as in monocotyledons, five and multiples of five is the rule. There are, however, numerous exceptions, as we shall see by-and-by.

PEDUNCLE AND BRACTS.

Before commencing to consider at length the various parts of the flower, and the way these flowers are arranged on the stem, it may be well to describe certain supplementary or variable parts connected with it—viz., the peduncle, and bracts and their modifications.

Peduncle.—The peduncle or flower-stalk, when present, is a veritable branch of the axis (axophyte), and may be either simple or branched. In the latter case the branches are called *pedicels.* As we shall see when discussing the inflorescence, there may be *primary, secondary,* and *tertiary* axes; and, in reference to its

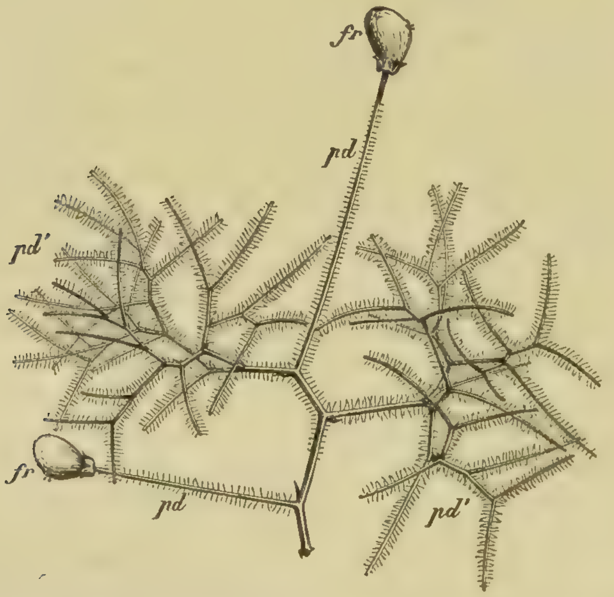


Fig. 142.—Plumose peduncles of the Wig tree (*Rhus Cotinus*, L.) *pd* Fertile peduncles; *fr* Fruits; *pd'* Sterile peduncles, branched and plumose.

position on the main axis, it may be *axillary* or *terminal*—*i. e.*, it may arise in the axil of a branch or at the end of a branch. Some peduncles, as in certain species of *Solanum*, come off opposite to leaves; but when speaking of the scorpioidal inflorescence, we shall return to this. Finally, peduncles may be unifloral, bifloral, trifloral, or multifloral, according as they bear one, two, three, or more flowers. In *shape* the peduncle varies, being cylindrical, compressed, and grooved. In the Cashew (*Anacardium occidentale*) it is the large succulent coloured expansion on which the nut is supported; while in *Vallisneria*, &c., it is spiral; and in *Alyssum spinosum* it is spiny. Peduncles may often branch, the branches being very numerous, and yet produce no flowers at their terminations, as in the case of *Rhus Cotinus* (fig. 142).

Receptacle.—This is the summit of the peduncle on which the floral organs rest, or to which they are attached—hence the name of *Thalamus* (bed) sometimes applied to it. In shape it may be conical (*Ranunculus*, Hellebore), flattened (*Cerastium*), or, as in *Nelumbium*, dilated into a large top-shaped body nearly enclosing the pistils, each in a separate cavity. In *Myosurus* the peduncle terminates in an elongated form, which in certain stages of the fruit causes the peduncle to look like a mouse's tail—hence the familiar name applied to the plant; while in the strawberry it is the expanded succulent receptacle which forms the well-known "fruit"—the real fruits, however, being only the minute carpels, familiarly called "seeds," attached to the surface of this swollen receptacle. In *Dorstenia* the flowers are immersed in an expanded receptacle (fig. 143). It occasionally happens that we find in plants—for example, *Solanum Guineense*, Lamk.—the peduncle arising apparently not from the axil of a leaf; but in

Fig. 143.—*Dorstenia Contrayerva*. *a* Entire plant in flower, showing also the "nodose" rhizome, which is used medicinally as a diaphoretic; *b* Flowers immersed in the receptacle.

the case of such an *extra axillary peduncle*, we find that in reality it is adherent to the axis for some distance, and only becomes free at the place from which it seems to spring. A less abnormal case is that in which the peduncle is united along the median line of the leaf from the axil of which it springs. Examples of these *epiphyllous* inflorescences are afforded by *Dulongia acuminata*, and notably by the remarkable Japanese shrub, *Helwingia rusciflora*.[1] In a Diosmaceous American plant of the genus *Erythrochiton* (*Hypophyllanthus*), the peduncle adheres to the under surface of the leaf, such an inflorescence being called by Planchon, who described this singular exception to the ordinary rule, *hypophyllous*.

It not unfrequently happens, as in the pinks, and markedly in *Silene*, that there is a considerable distance between the calyx and corolla, by the development of the internode between them; so that a stalk on which the rest of the flower is borne is formed within the calyx. Again, in Gentians the fruit is borne on a stalk by the formation of an internode between the stamens and pistil. This kind of stalk is called a *stipe*, and the organ or set of organs thus elevated is said to be stipitate. If it elevates the petals, stamens, and pistils, it is called the *anthophore* (flower-bearer), as in *Saponaria officinalis* (fig. 145); the *gonophore* when it supports both stamens and pistils, as in the passion-flower (fig. 144), Capers,

Fig. 144.—*Passiflora Loudoniana*, Hort., entire flower. *d d* Numerous corolline filaments; *e e* Stamens; *p* Pistils borne on the *gonophore*.

---

[1] Of W. Dans, Osyris Japonica of Thunberg; see Decaisne in Ann. des. Sc. Nat. vi., 1836, p. 65-76, pl. 7.

Magnolia (fig. 146), &c.; and the *gynophore*, *gynobase*, or *carophore* when, as is most common, it bears the gynœcium alone. The stalk, which sometimes supports each simple pistil or carpel of the gynœcium, as in *Coptis*, is called a *thecaphore*.[1] This does not, however, in reality belong to the receptacle at all, but to the pistil itself, and is homologous with the leaf-stalk.[2]

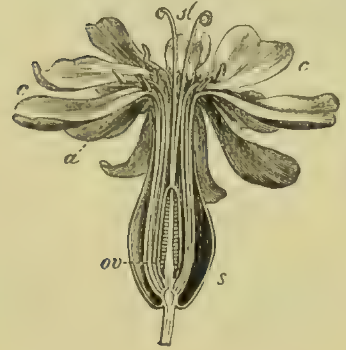


Fig. 145.—Longitudinal section of *Saponaria officinalis*, L. (Soapwort), with a semi-double flower. *s* Calyx; *c c* Petals furnished with appendages or lamellæ *a*; *st* Styles; *ov* Ovary. The corolla, stamens, and pistils borne on the *anthophore*.

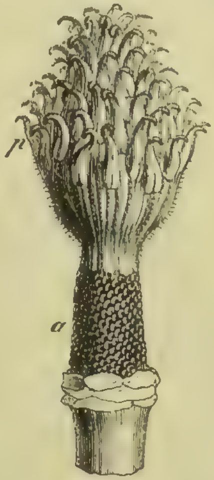


Fig. 146.—*Magnolia grandiflora*, L. Mass of pistils or carpels of pistils, *p*, supported by a large long *gynophore* (*a*).

Bracts.—In many plants the flowers spring from the axils of leaves (floral leaves) differing in no appreciable degree from ordinary leaves. But in others the leaves from the axil of which the flowers rise have a regular gradation from ordinary leaves up to what are called *bracts*—these bracts being, however, veritable leaves, which, as they ascend the stem, change their form and coloration, until the uppermost ones not unfrequently assume the appearance of petals. In being entire or divided, bracts also ape the nature of leaves. In position they likewise affect the character of leaves, being *alternate*, *opposite*, or *verticillate*. Though ordinarily they have the same phyllotaxis as the leaves of the plant on which they are found, yet it will occasionally happen that a different arrangement will present itself. For instance, in *Campanula erinus* the leaves are alternate and the bracts opposite.

---

[1] Under the special name of *Podogyne*, Mirbel has described a long narrow extension of the base of the ovary in *Astragalus galegiformis* and a great number of other *Leguminosæ;* but to apply a separate name to a thicker or thinner portion of the same organ, and then a separate name to the organ (or in the case of a fruit) so shaped, is the *reductio ad absurdum* of name-making.

[2] Gray, lib. cit., 267.

Occasionally these bracts will attain a great development, and a brilliancy exceeding that of the flowers themselves. This is seen in the bracts of *Salvia fulgens*, *Amherstia nobilis*, *Poinsettia pulcherrima*, *Bougainvillea spectabilis*, *Musa coccinea*, and various of the Bromeliaceæ or pine-apple order. The linden supplies an excellent example of the nature of a bract. In fig. 147, *f*, is the normal leaf, and *b* the bract of a linden (*Tilia platyphylla*, Scop.); *pd* the peduncle, bearing the two fruits *fr*, attached in its inferior portion *pd'* to the midrib of the bract. (The student's attention may also be called to the fact that the two sides (*a a'*) of the normal leaf of the lime are unequal.) In some species the stem above the place from which the flower arises bears several bright-coloured bracts, gathered into a terminal tuft (coma), as seen in *Salvia Horminum*, *Lavandula Stœchas*, *Ananassa sativa* (pine-apple), &c. Accordingly, in such plants the bracts have no flower-buds in their axes. In *Barleria* and *Exoacantha* the bracts are transformed into spines, and in *Bauhinia* into tendrils.

Fig. 147.—Leaf and fruit of Linden (*Tilia platyphylla*), with bract.

Bracteoles.—Suppose, now, that in addition to the bract, as figured in *Tilia*, there was another smaller one inside of it, and at the base of the ramifications of the peduncle (*pedicels*), this would be called a *bracteole*, or little bract.

Involucre.—We have seen that a flower or a flowering branch may spring from the axils of a bract. Now, if a stem terminates by a number of peduncles, or by flowers very close together which seem to end about the same level, the bracts will be equally arranged around the same point, and will form an envelope surrounding its base : this is an *involucre.* There are two kinds of involucres : 1. In *compositæ.* In this order of plants a great number of small florets are placed together, and at about a common level on the summit of an expanded peduncle (as is seen in the daisy, dandelion, &c.) ; hence the older botanists called such plants composite plants, and the name has been applied to the great order Compositæ (figs. 148, 150). All these florets are enveloped by a number of bracts, to which L. C. Richard applied the name of *Periphoranthium*, Cassini that of *Periclenium*, and

Linnæus, first of all, that of the *common calyx*. The term *involucre* is now more commonly used. This general involucre of compositæ presents, however, various forms, which have been used by systematic botanists to furnish characters for the division of this extensive order into smaller groups. For instance, it is often (α) *scaly;* in other cases the bracts are (β) superimposed and imbricated (fig. 149); (γ) in *Helminthia echiöides*, Gært., *Senecio* (groundsel), &c., the involucre is surrounded at the base by a row of bracts like a calicula around a calyx, hence such bracts have been styled *caliculated;* (δ) lastly, there may be a single verticil of bracts with their edges, when they come in contact with each other, united so as to appear like a gamosepalous calyx (p. 304), as in species of *Buplevrum*, *Lavatera*, &c., such bracts being called *gamophyllous*, in contradistinction to the opposite case of *polyphyllous* bracts. The bracts of an involucre may, like ordinary leaves, be terminated by spines, hooks, &c., as seen in thistles (*Carduus*), Burdock (*Arctium Lappa*), teasel (*Dipsacus*) — this

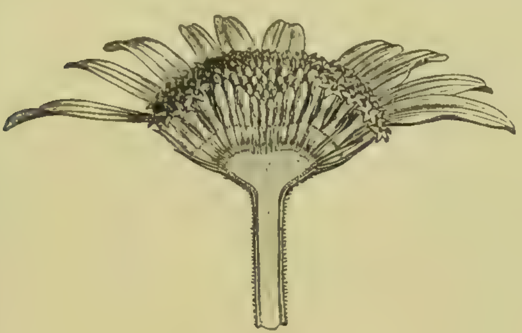


Fig. 148.—*Anthemis rigescens*, W., one of a group of flowers called "Compositæ," or "composite flowers," cut in a longitudinal section to show the numerous flowers of which the capitulum is composed (nat. size).

Fig. 149.—Flower or capitulum of a Thistle (*Carduus pycnocephalus*, D.C.), entire, with the imbricated involucre.

Fig. 150.—Capitulum or flower-head of *Eryngium campestre*, in longitudinal section, showing the large involucre.

character in one of the last-named genus, the fuller's teasel (*D. fullonum*), having caused it at one time to be used in carding, &c. 2. In *Umbelliferæ*, a large order to which the hemlock-like plants belong, we find the second division of involucres. In this order we find a general involucre (the *collerette* of the French botanists) round the main, and several little *involucelles* around the base of each secondary umbel or umbellule (*Ex.*, the carrot). In some plants of this order (*Angelica*, *Scandix*, *Chærophyllum*, &c.) the involucre disappears, and only the involucelles remain.

In a few (*e. g.*, *Pastinacea sativa*, L.) it is reduced to one or two bracts; while in a third set they fall off entirely, leaving the umbel *naked* (*e. g.*, *Pimpinella Anisum*, L.), the fennel (*Fœniculum officinale*, All.), &c.

Though involucres generally surround several flowers (in which case they are *plurifloral*, yet instances are not wanting in which there is only a single flower surrounded by an involucre. Such a case of *unifloral* involucres is exhibited in *Nigella damascena*, L. In the common hepatica (*Anemone Hepatica*) the involucre looks very like a calyx, and indeed has been so described by some botanists, though it is usually styled a *calyciform involucre*. It, however, by insensible degrees, graduates into the ordinary plurifloral involucre, seen in various other members of the same genus and order.

Calicula.—Occasionally we have at the base of the calyx several bracts in union, the divisions being either the same number as the divisions of the calyx, and alternating with them, or a different number. Fig. 151, showing an entire flower of an Indian strawberry (*Fragaria Indica*, Andr.), gives an example of the first case. In this plant the calicula is much larger than the calyx itself.

Fig. 151.—Entire flower of *Fragaria Indica*. *s s s* Calyx; *i i i i i* Bracts forming a calicula (1/1).

Our common strawberry, as well as the allied genera, *Geum*, *Potentilla*, &c., possesses an analogous calicula, but much smaller, and apparently, on first sight, differently arranged.

The second form of calicula—viz., in which the divisions of the calicula are generally in number different from and non-alternating with the divisions of the calyx—is seen in the mallows and the greater number of the genera of the order *Malvaceæ*. In these plants the divisions of the calicula are rarely equal to the divisions of the calyx, and are sometimes free, sometimes united one to another in such a manner as to appear like a second gamosepalous calyx. The latter kind of calicula is frequently styled by descriptive botanists *regular* or *calyciform calicula;* but, strictly speaking, the term would be more applicable to the first kind. Among the pinks (*Dianthus*), and especially in *Dianthus barbatus* (fig. 152), we find an *imbricated* calicula. In the figure it will be seen that the calicula is composed of six bracts, rather expanded inferiorly and attenuated superiorly, arranged in three pairs, which overlap each other. In the ordinary cultivated garden pinks, a curious monstrosity is often seen; the bracts become numerous, and overlap each other in many pairs, while at the same time the flower becomes badly developed, or atrophied.[1]


Fig. 152.—Entire flower of *Dianthus barbatus*, L., with an *imbricated* calicula of six bracts (1/1).

Cupula.[2]—This form of bract is familiarly seen in the acorn of the oak. The cup, which surrounds the gland or acorn, is an involucre of little bracts, which, after having covered many flowers, remains, and accompanies the fruit, which it either partially or entirely covers.

This cupula only covers the female flowers. The "scales" of the cup, which differ in form in different species, are the bracts. In the species figured (fig. 153), the cups are, on account of their richness in tannin, used for dyeing black.

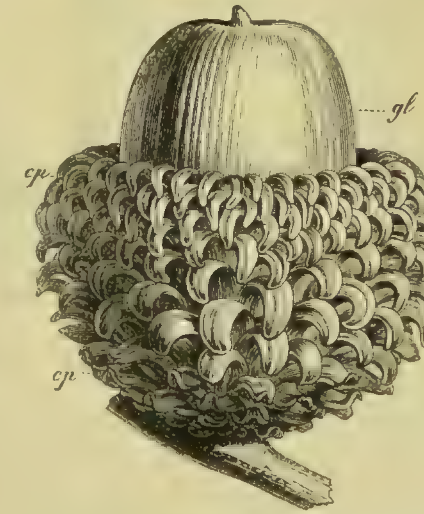


Fig. 153.—Gland, *gl*, of *Quercus Ægilops*, L., surrounded on the lower portion by a cupula of foliaceous bracts, *cp* (nat. size).

In the chestnut, as well as in some of the "overcup" oaks, the cupula quite surrounds the fruit, when it is said to be *pericarpoïdal—i. e.*, having the appearance of a pericarp or wall of a fruit.

Spathe.—Hitherto we have only spoken of bracts as seen in Dicotyledons; the remaining four which we shall describe are found among the Monocotyledons. This is the large sheathing bract which surrounds the flowers of various monocotyledonous plants, and may be either composed of one bract (*univalvular* or *monophyllous*) or of two (bivalvular or diphyllous). Palms, Araceæ (fig. 154), Iris, Narcissus, &c., all show excellent examples of the spathe.

---

[1] Duchartre, l. c., p. 452.

[2] Little cup.

Spathellæ are the little spathes surrounding each subdivision of the general inflorescence, surrounded by a common spathe, as in the palms.

The spathe may present great differences in form, in dimensions, in coloration (being either *herbaceous* or of bright colours), in consistence (*foliaceous*, *thin*, *dry*, *scarious*, or completely *woody*, as in some palms), or it may contain one, two, three, or a number of flowers (*unifloral*, *bifloral*, *trifloral*, and *multifloral*). In some palms, when it may reach a length of more than 20 feet, the spathe may embrace as many as 20,000 flowers. The spathe frequently (as in the case of palms, Pothos, Typha, &c.) becomes caducous after the flowers which it protects in the young state have become developed.

Fig. 154.—*Arum maculatum* (Cuckoo-spit), one of the Araceæ, showing the spathe (*a*) and the spadix (*b*).

Glume and Glumella.—By most authors these are considered of the nature of bracts, and are seen in grasses and *Cyperaceæ*, where they play a part analogous to that of the perianth of many other monocotyledonous plants (figs. 168, 169). The flowers of grasses are attached in distichous order on a common axis in little groups called *spikelets*, which in several genera consist of but a single flower, and which are distributed along the stem in various ways (fig. 170). The common rye-grass (*Lolium perenne*, L.) supplies a good typical example of the way these spikelets are arranged on the common axis.

Each of these spikelets is enclosed within two bracts, placed opposite one another, but attached, the one a little below the other. This common envelope constitutes the *glumes*.[1]

Again, each floret is enclosed within its own proper envelope or scales, which has been called a *glumella*.[2] The two leaflets or *paleæ* of this glumella are unequal in size. The exterior one is (fig. 155) the largest, and is ordinarily green and firm, and provided with a median nerve, and lateral symmetrical nervules of unequal number. Accordingly, it has been called *imparinerved palea*. The one next to the axis is, on the other hand, thin, dry, translucent, smaller, and placed a little higher up, and shows, in the opinion of Schleiden, Duchartre, and other botanists, that the glumella is not, as Robert Brown thought, "a floral envelope, comparable to what is seen in the flower of phanerogamia in general," but only two leaflets, which bear the relation of bracteoles to the bracts which form the glume. This internal palea, on account of the two symmetrical nerves which are seen in it, has been called the *parinerved palea*. Finally, the singular floral structure of the gramineæ is further complicated by the presence of an interior circle, composed of rarely three, but often of two, little scales, situated a little in front of the external palea; these are (fig. 155, *sq*) the *paleolæ*, *squamulæ*, *glumellulæ*, or *lodiculæ* (De Beauv.) Many botanists are inclined to look upon these as the true perianth of grasses (Duchartre).

Fig. 155.—Part of the flower of a grass. *p* External palea, with the internal one removed, to show, *sq*, the lodiculæ or squamulæ; *st* style; *a* Anthers.

Ordinary bracts frequently fall off when the bud in their axil expands; and in some Boriganaceæ, and in most of the Cruciferæ,

---

[1] Of Jussieu (*glumæ*, Latin); the *calyx* of grasses and cyperaceæ of Linnæus; the *lépicene* of Achille Richard; the *bâle* (French) or *tegmen* (Latin) of Palisot de Beauvois; the *peristachyum* of Panzer; the *perianthelium* of Petermann.

[2] By Link, Mirbel, and others; Linnæus called it a *corolla*, and Robert Brown, who looked upon it as a true floral envelope, gave to it the name of *perianth*; De Candolle and his followers named it the *perigonium*, while De Beauvois named it the *stragulum* (stragule).

they are entirely wanting, such inflorescences being termed *ebracteated.* The outer bracts of involucres do not generally produce flower-buds, but, as in the case of the "hen and chicken daisy," this may occasionally happen ; and it may also occasionally happen that, as in the case of viviparous flowers, the axils of the bracts, instead of giving rise to flower-buds, produce leaves instead—such a monstrosity showing, amid many other proofs, that the flower-bud is only a metamorphosed leaf-bud.

We will now consider each of the floral whorls more in detail; but before doing so, we may profitably discuss the nature of the operation known as *flowering.*

FLOWERING.

Flowering an exhaustive process.—Flowering is directly antipathetic to nourishment—plants, as a rule, flowering in a ratio inverse to that of their luxuriance of growth. Take, for example, maize or Indian corn. For its successful cultivation, a mean summer temperature of 65° Fahr. is required, with a mean 2° higher in July. In southern latitudes the warm spring develops the juices of the Indian corn too rapidly; and accordingly it runs to leaf and stalk, to the neglect of the seed. In the West Indies, for instance, it rises 22 feet in height, but produces only a few grains at the bottom of a spongy "cob" too coarse for human food. In the Southern United States the corn grows to the height of 15 feet; but the produce is much less than in the Northern States, where the stalk is only from 7 to 10 feet. Hence, in order to make a tree or bush bear fruit, it must be pruned, otherwise the nourishment which was necessary to produce the flower goes to nourish the luxuriant growth of wood and leaf. Again, the gardener girdles a tree in order to make it bear fruit more luxuriantly; in other words, he cuts off a ring of bark, by which the descending (elaborated) sap is kept in the branches above the "girdle"—the result being that these branches bear fruit abundantly, while the shoots below do not blossom, but send out leafy branches. For a similar reason, as Gray remarks, the flowers of most trees and shrubs which bear large or fleshy fruits are produced from lateral buds resting directly upon the wood of the previous year, in which a quantity of nutritive matter is deposited. So, also, a seedling shoot which would not flower for several years, if left to itself, blossoms the next season when inserted as a graft on to an older trunk, from whose accumulated stock it draws. Accordingly, the student must see that flowering is an exhaustive process, requiring as it does such a large amount of nourishment; yet if the plant is placed in too rich soil, it either rots or runs off to leaf without bearing flowers. *Annuals* flower within a few weeks of the time the seed is placed in the soil, and so soon exhaust themselves. *Biennials*, again, soon exhaust the supply of nourishment stored up in the roots; while shrubs and trees do not flower until they are strong enough to bear this strain on their constitution, and hence are *perennials*. Linnæus remarked that however hardy a biennial might be before flowering, it perishes at the approach of the succeeding winter; nor can artificial heat preserve them. This is attributed to exhaustion of the vital forces by flowering. Several perennial or even shrubby plants of hot climates, become annual in our gardens — *e. g.*, *Tropæolum* or Indian cress, *Mirabilis Jalapa*, &c. On the other hand, some biennials flower and fruit their first year, and thus become annuals—as, for example, according to Thilo Irmisch, is often seen in *Melilotus dentata* and *Echinospermum Lappula*. According to Duchartre, the black henbane (*Hyoscyamus niger*), which is normally a biennial, has been known to become annual; and these individuals have been described as a distinct species under the name of *H. agrestis*. The age of a plant has also an effect on flowering, and some plants have a predisposition to flower early. For instance, the "Bengal roses" (*Rosa sempervirens* and *Indica*) flower before the seminal leaves have died away.[1] Feebleness of constitution, also, sometimes assists in causing the plant to flower, while excess of vigour injures it in this respect. Hence plants brought from a distant country will often flower immediately after a sea voyage, though not for a long time again. Gardeners take advantage of this peculiarity, and by arresting the vigour of a plant secure flowers, when otherwise they would not have been produced. If a tree, especially of a late-fruiting variety, bears an excessively abundant crop of fruit one year, it will often bear none the next year. This peculiarity is equally seen among wild as among cultivated plants. On the other hand, if no fruit appear one year, the tree will accumulate strength, and most probably bear abundantly next season. How exhaustive a process flowering is we see in biennials like the turnip and carrot. The edible portion of both these plants contains the store of nourishment accumulated for the nutrition of the flowering plant. After the plant has flowered, we see that it has quite exhausted this store in addition to what it had taken up directly from the soil. The farmer accordingly, unless he wishes to obtain seed, takes his "root crops" out of the soil before they have flowered. Again, the bamboo, a gigantic grass of intertropical countries, after attaining a height of 60 or 70 feet, flowers and

---

[1] Early flowering sometimes occurs as exceptional cases in plants. For instance, in the 'Gardeners' Chronicle,' 1873, p. 213, is figured a cocoa-nut palm from Bengal producing flowers of both sexes while still in the seedling state, though these trees do not naturally produce their flowers until they have attained some age and size.

fruits, and then perishes. The sugar-planter is also well aware of this, and cuts the canes before they flower, otherwise the saccharine juice would be consumed in supporting the strain on the plant's constitution. We see a practical application of these facts in the horticulturist being able to convert annuals into biennials, or even to prolong the life of the plant indefinitely, by not allowing it to seed; but if once the plant is allowed to seed, whether this may be in the first or second year, the result is the same—the plant's existence is over. For example, the common garden larkspur has given origin to a double-flowered variety, which of course bears no seed, and has therefore become a perennial instead of an annual. The common mignonette (*Reseda odorata*) can thus be converted into a perennial by preventing its seeding. Cabbage-stumps planted for seed, it is also affirmed, may be made to bear heads the second year by destroying the flower-shoots as they arise; and if the process is continued year after year, the result will be that an annual plant, as the cabbage naturally is, will be converted into a kind of perennial. Again, the *Agave Americana*, or "century plant," so called because in our conservatories it only flowers about once in 100 years,[1] flowers in the warm climate of its native Mexico when only 5 or 6 years old; but the process is so exhausting, that to nourish the large flower, the juice (fermented under the name of "pulque" and "mescal") is exhausted, and the plant perishes after flowering and maturing its fruit. The large Talipot palm (Corypha), which grows to a great height, bears immense clusters of flowers, and produces a great crop of nuts. The effort of so doing is, however, too much for it, and the tree perishes after the first season. Flowering, therefore, differs from the production of foliage in so far that it consumes the stored-up products of the plant without giving anything in return. Instead of taking CO_2 from, it gives back CO_2 and water to, the air. The flowering is the most exhaustive of the reproductive processes, though fruiting is also somewhat exhausting. In the fruit and seed, however, the nutriment is stored up in a concentrated form for the future use of the new individual in the seed—viz., the embryo plant. Flowering is also accompanied by an evolution of heat considerably over the normal temperature of the plant, owing to the fact that "when carbon is consumed as fuel, and the oxygen of the air converted into CO_2, an amount of heat is evolved duly proportionate to the quantity of carbon consumed, or of CO_2 produced" (SECTION IV.)

A period of rest is needed.—If a plant leafs too luxuriantly, or is grown in too rich a soil, there is often no seed produced. Hence Northern trees transplanted to the tropics often do not flower;

---

[1] This is a somewhat arbitrary popular generalisation. The truth is, that it only flowers once in a *great* number of years, generally once in 50 or 60.

and transplanted trees generally flower the first year after their transplantation, though not a second time until after a long interval, because during the first year there has been a check to their growth, owing to the transplantation. However, if the tree is not injured or checked in transplantation, the contrary fact is true. A period of rest is required after flowering. This season of rest is supplied by the dead season of winter and autumn, in which latter period most of the trees and shrubs, and other perennial plants of temperate climates, form the flower-buds for the ensuing year. In the tropics, again, the dry season supplies the necessary season of rest. In the Canary Islands, the growing season is from November to March—the mean temperature of this season, corresponding to our winter, being 66° Fahr.; while that of the summer (April to October), when it seldom rains, is as high as 73° Fahr. During this season the soil is baked like a brick, and with the exception of the succulent plants, vegetation almost disappears. Thus the dry season brings a period of repose to plants, just as the cold season does in our climate—" the roots and bulbs lie dormant beneath the sunburnt crust, just as they do in our frozen soil. When the rainy season sets in, and the crust is softened by moisture, they are incited into growth under a diminished temperature, just as with us by heat; and the ready-formed flower-buds are suddenly developed, clothing at once the arid waste with a profusion of blossoms. The vegetation of such regions consists mainly of succulent plants, which are able to live through the drought and exposure; of bulbous plants, which run through their course before the drought becomes severe, then lose their foliage, while the bud remains quiescent, safely protected under ground until the rainy season returns; and of annuals, which make their whole growth in a few weeks, and ripen their seeds, in which the species securely passes the arid season."—(Gray.)

Heat is one of the most powerful of the *exterior* influences exerted on flowering. Each species has a mean temperature or a *sum* of degrees necessary for flowering. Thus Gasparini has, in a table from which the following examples are culled, given the following as specimens of the mean heat required for the flowering of certain plants :—

	Fahr.		Fahr.
Hazel,	37°4	Robinia,	57°2
Peach,	41°0[1]	Barley, wheat,	60°8
Apricot, almond,	42°8	Chestnut,	62°6
Cherry, pear, &c.,	46°4	Vine,	64°4
Lilac,	48°2	Maize, olive, &c.,	66°2

It is not easy to give the *sum of degrees* of heat necessary for the flowering of all plants in regard to which calculations have been

---

[1] The degrees Centigrade are not reduced to the hundredths of a degree.

made, as different writers take different methods of calculating it. In the same country and the same year, a plant often flowers late or early, according to the degree of heat it is subjected to;[1] while the same species growing in different countries opens late or early, according as the country may happen to be north or south, or be hot or cold. Schubler says that each degree of latitude influences the time of flowering of a particular species a quarter of a day; and this difference of time in flowering has, of course, an equal influence on the fruiting of the species.[2] Dryness also affects flowering in this respect, that wet increases the foliage, and therefore acts indirectly in moderating the flower. Hence Britain and other equally damp countries—particularly the "Emerald Isle"—are specially distinguished for the green luxuriance of their vegetation, in comparison with dry countries. The gardener can accordingly take advantage of these facts to vary the influences under which he desires to place the plants in his conservatories, according as he wishes to obtain early or late flowers and fruits. "Forcing," for instance, is only an application of the foregoing principles, and consists in a skilful alternation of the periods of repose, by subjecting a plant to heat in a hothouse at one season, and cold in a frigidarium at another. The cultivator thus gives plants an artificial season of rest by the application of cold; and then by the influence of heat, light, and moisture, causes it to grow at a season when it would have been quiescent. Thus at will he retards the periods of flowering and of rest, so as in time to completely invert them. Lastly, each plant flowers at a particular season, and opens and closes at particular hours; but this we shall have occasion to discuss in subsequent pages—(SECTION IV.)

---

[1] See the very instructive reports on this subject, so far as regards the flowering of plants in the Edinburgh Botanic Gardens, by Mr James M'Nab, in Trans. Bot. Soc. Edin. (*passim*).

[2] See for further discussion of this question the subject of PHYTO-GEOGRAPHY.

CHAPTER II.

THE PERIANTH, OR FLORAL ENVELOPES.

In a perfect flower there are four whorls of organs—viz., the pistil, the stamens, the corolla, and the calyx. The *Calyx*[1] is the most external of the four, and, in common with the corolla, constitutes the *Perianth* or *Perigone*,[2] or envelopes which surround the essential reproductive organs—viz., the stamens and pistils—and, like the corolla, may be either absent or present. In *Dichlamydeous*[3] plants, both calyx and corolla are present; in *Monochlamydeous*[4] only one, the calyx, remains; while in *Achlamydeous*[5] plants, both calyx and corolla are absent. The segments of the calyx in most cases alternate with the segments of the corolla.

CALYX.

The calyx is composed of leaf-like divisions called *sepals*[6]—these sepals being either coalesced with each other wholly or in part, or distinct.

Form and Nervation of Sepals.—In appearance the sepals are not unlike the scales surrounding buds. In shape they vary little. They are generally more or less ovoid, entire, or slightly dentate or crenulate, and rarely[7] deeply divided. To the forms and divisions of the margins of sepals, the terms used in the description of leaves are also applicable, so far as necessary. Thus sepals may be *winged*, *obtuse*, *lanceolate*, *cordiform*, &c.; and their varieties in shape are occasionally used as characters for species.

The *nervation* of sepals is usually simple, and corresponds to that of the leaves of the species of plants to which the calyx belongs. In Dicotyledons, the venation of the sepals is accordingly usually netted, and in Monocotyledons parallel, the paren-

---

[1] *Calyx*, a cup; plural *calyces*. I prefer using the Latin plural rather than the barbarous English "calyxes."

[2] περὶ, around; ἄνθος, flower: περὶ, γόνος, reproduction.

[3] δις, twice; χλαμύς, a covering. [4] μονος, one. [5] α, privative.

[6] *Sepio*, I enclose; also called *foliola*, *phylla*, or *calycine leaves*.

[7] As in *Perganum Harmala* (Syrian rue).

chyma being placed between the vascular bundles, and each side covered with an epidermis, differing in no appreciable manner from the corresponding tissue in the leaves. Each sepal is usually sessile, but in a few cases (*Tropæolum* or Indian cress, fig. 182) it is prolonged into a spur (*calcar*), or enlarged so as to form a hood or helmet (*galea*), which covers up the flower like a cowl (as in Aconite or "Monk's-hood"). Sometimes in the violet and mouse-tail (*Myosurus minimus*) each sepal posesses a peculiar appendage, arising from it just where it is attached to the receptacle, and prolonged downward along, but without adhering to, the peduncle.

Pappus or Aigrette.—In the order *Valerianaceæ*, and in most *compositæ*, the calyx is reduced to a tuft of hairs called a *pappus*, (fig. 156, *b*) in which, at first sight, it seems difficult to recognise the calyx at all, until we find certain plants, where we can trace all gradations between the ordinary form of calyx and the pappus, as may be seen by examining *Gaillardia picta*, *Catananche cærulea*, and *Scabiosa atro-purpurea*—the first and last of these plants presenting the two extremes, and the second-named one the medium between the forms of calyx. Each "hair" of this tuft-like calyx or aigrette may be either simple or plumose (fig. 156, *c*) by the presence of secondary barblets along its side.

Fig. 156.—*Carlina subacaulis*, one of the Compositæ, distinguished by the large development of the scales of the involucre. Fruit, *b*, terminating in a pappus ; *a* Tubular floret surrounded by its aigrette-like calyx (pappus); *c* Magnified view of one of the "hairs" of the pappus.

Mode of Insertion of Sepals.—They are generally attached to the receptacle horizontally, leaving, when detached, a cicatrix shaped like the arc of a circle or a horse-shoe. In the mode of insertion of the sepals there are, however, several minor modifications, though none are of any very great importance. An examination of the calyces of *Cytisus hypocistis*, *Pelargonium*, *Erisma violacea*, &c., will afford examples of several such.

Morphological Nature of Sepals.—Between leaves and bracts we have seen there are regular gradations. So also we find an equal transition from the bract to the sepal, so that it is different to say where the bract ends and the sepal begins. Take, for example, the bud of a *Camellia*. It is really impossible to distinguish, so far as form, nervation, and structure are concerned, the five sepals from the numerous bracts which surround them. Take, again, the ordinary hundred-leaved rose. Here we find the bud surrounded by five sepals. These sepals have the inferior extremity of each expanded in a petiole-like portion, to each side of two of which are attached two little leaflets, in form and shape exactly like stipules. The third one has only one of these stipule-like appendages, while the remaining two are entirely deprived of any such appendages.[1]

The sepals, we see, are thus simply modified leaves, just as we have seen are the bud-scales and bracts; and, as we shall by-and-by show, are also the petals, stamens, and pistil—an idea first conceived by Linnæus,[2] again broached by Adanson, but which the genius of Goethe carried out in all its beauty. In any case in which there is a difficulty in determining which is calyx and which bract, it is better to consider the calyx the organ nearest the flower, and the bract that which is situated further down the peduncle. Finally, we may remark that the calyx is sometimes not equally developed in all the flowers of the same inflorescence. For instance, in the wild *Hortensia* the calyces of the flowers at the circumference of the inflorescence are very large, while those in the interior have them developed only to a small extent.

Duration of the Calyx.—The calyx may be *caducous* when it falls immediately after the flower has expanded (poppy, fumitory), or when the fruit commences to form (wallflower, turnip); and *marcescent* when it remains persistent in a withered state after the blossoming of the flower, and accompanies the fruit during its growth. In *Gaultheria* (the salal of the Western American woods), *Muhlenbergia*, and mulberry (*Morus nigra*), it even takes a fleshy consistence, and forms the chief edible portion of the "fruits" so

---

[1] Hence the following distich:—

"Quinque sumus fratres, unus barbatus et alter,
Imberbesque duo; sum semiberbis ego."

[2] "Prolepsis Plantarum" (Amœnitates Academicæ, Ed. Schreb., vi. 324).

called of these plants; or, as in the case of *Physalis Alkekengi* (winter cherry), it may take a considerable increase, though still remaining in a membranous condition.[1] Another form of persistent calyx is seen in roses; here it not only remains, but takes a marked increase and development while the fruit is growing. Such a calyx is called *accrescent*. In the figure of *Rosa alba*—the common white rose of our gardens—(figs. 157, 158), we see that the calyx is expanded into an ovoid tube, surmounted by five elongated lobes. Slowly this "calycinal tube" increases, and its walls thicken, and become reddish-orange coloured, as familiarly seen in the "hip" of the roses, which is, however, not the fruit—the true fruits being what are commonly taken for seeds inside this fleshy tubular expanded calyx.[2] As a rule, a calyx composed of several sepals, all disunited, is caducous; while one in which they are united into a single tube is marcescent.

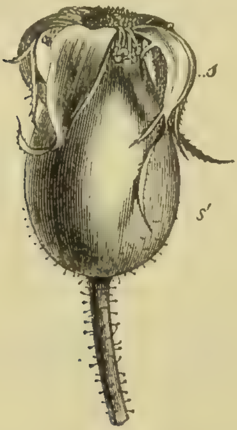


Fig. 157.—Thickened and expanded calyx around the fruits of *Rosa alba*, L. *s* Blade of one of the sepals; *s'* Tube of the calyx.

Fig. 158.—Longitudinal section of the same. *s* Blade of one of the sepals; *s'* Tube of the calyx; *fr* Fruits; *e* Withered stamens (nat. size).

Calyx, Regular or Irregular.—When the sepals or the divisions of the calyx are in all their parts equal among themselves, and symmetrically disposed around the centre of the verticil, then the calyx is said to be *regular*; if the contrary is the case, then the term *irregular* is applied to it. The fuchsia, tobacco, &c. (fig. 160), are examples of the first kind; the milkwort (*Polygala vulgaris*) affords a specimen of the second kind of calyx (fig. 163).

---

[1] This large membranous orange pouch around the fruit of *Physalis* has, by some botanists, been called an *induvium*, and the term *induvial* has therefore been applied to this description of calyx.

[2] By some botanists the calycinal tube is looked upon as an expansion of the peduncle. According to this view, the true calyx would be the sepals surmounting it.

The calyx, when the divisions are not soldered together, may be composed of several sepals, though in general six is the maximum number. Thus there are two in the poppy; three in the lesser celandine (*Ranunculus Ficaria*); four in the wallflower (*Cheiranthus Cheiri*) and other Cruciferæ; and five in the common buttercup (*Ranunculus acris*, &c.)—the terms *Di- Tri- Tetra- Penta- sepalous*, &c., being used to express such numbers of sepals.

Calyx, Dialysepalous and Gamosepalous.—When there is more than one sepal in the calyx—the sepals being all distinct from each other—then the term *dialysepalous*[1] is applied to it. On the contrary, if the sepals are united together, either throughout a part or along the entire contiguous margin of each sepal, then the contrary term of *gamosepalous*[2] (figs. 159, 160) is used to express this peculiarity. In the latter case, the number of sepals of which the calyx normally consists may be generally detected by observing the number of divisions or segments which surmount the top of such a gamosepalous corolla. Sometimes the sepals are only united at their base—the united portion forming a continuous ring; while the laminæ of the sepals are entirely free. In other cases they may be less deeply divided; while in a third example, the divisions may not extend beyond a slight indentation on the top of the calyx. In order to express the extent of this division, the same term used to describe the margins of leaves may be employed, though, in the present case, the divisions of the upper edge of the gamosepalous corolla are entirely different in their character, being due to a totally different cause. Thus a gamosepalous calyx is *partite* when the sepals are only united at the base, thus remaining almost free; and, according to the number of such divisions, the adjective is further qualified by the terms *bi*, *tri*, *quadri*, *quinque*, *multi*, &c. (figs. 159-164), according as there

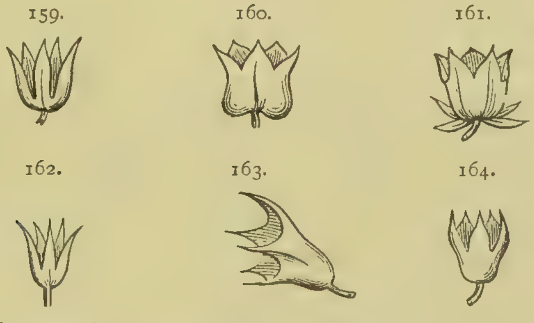


Fig. 159.—Quinquepartite regular gamosepalous calyx. Fig. 160.—Quinquedentate gamosepalous calyx. Fig. 161.—Epi-calyx. Fig. 162.—Regular calyx. Fig. 163.—Irregular calyx. Fig. 164.—Cleft calyx.

---

[1] Also called *Polysepalous* and *Polyphyllous*.

[2] γάμος, marriage; and φυλλον: also called *monosepalous* and *gamophyllous*.

may be two, three, four, five, or a greater number of divisions. It is *cleft* when the sepals are united for almost half their length (fig. 164), the termination *fid* being used to express this kind of division; thus a calyx is said to be *bifid*, *trifid*, *quadrifid*, *quinquefid*, *multifid*, &c. Thirdly, when the sepals are almost united through their entire length, they are said to be dentate; and, according to the number of divisions, are said to be *bidentate*, *tridentate*, *quadridentate*, *quinquedentate*, &c. Lastly, as in the honeysuckle, and most Umbelliferæ, the superior margin may be *entire*. In a gamosepalous calyx we distinguish three parts—viz., 1st, the *base*, or the part which is soldered together; 2d, the *tube*; 3d, the upper portion, or *limb* or lamina, formed by the free portion of the sepals; 4th, and lastly, the throat, or that portion represented by the line of separation between the tube and the limb. Hence in describing species the tube is said to be *cylindrical*, *compressed*, *angular*, *short*, or *long*; the limb *bidentate*, *bifid*, *bipartite*, *entire*, &c. Viewing the gamosepalous calyx as a whole, it may be *tubular* (as in most *Labiatæ*), *cylindrical*, *angular*, *cupuliform* (as in the orange), *urceolate* (as in the *Silene inflata*), &c.

Regular or Irregular Dialysepalous Calyx.—When all the divisions of a dialysepalous corolla are equal in size (as in the wallflower), it is said to be *regular*. When the contrary is the case, or when the sepals are united at different heights on the receptacle, or follow in their arrangement no certain law, then they are said to be *irregular*.

Regular or Irregular Gamosepalous Calyx. — When the divisions are all equal among themselves, or inserted at the same heights—by each portion of their united base—upon the receptacle, a gamosepalous corolla is said to be *regular*; and even though such conditions do not exist, still, in botanical language, such a calyx is said to be regular, provided such irregularities follow some uniform law. If the contrary conditions are present, the calyx is *irregular* (fig. 163). It may, however, happen, that even though the sepals or divisions of such a gamosepalous corolla may be equal, and attached at the same height and at equal distances on the receptacle, it must be irregular *if they are not all united together at the same height* (Payer).

Colour of Calyx.—It is in most cases of a more or less intense green; but there are numerous instances in which it is otherwise—*e.g.*, yellow in the Indian cress, red in the pomegranate (*Punica Granatum*), *Salvia splendens*, and fuchsia, though in the latter plant it is occasionally white. Such coloured calyces are called *petaloid*, from their likeness to the petals of the corolla.

Peculiar Calyces.—In the Australian *Eucalyptus*,[1] or gum-tree,

---

[1] εὖ, well; and καλυπτω, I cover: hence the term *calyptrate*, applied to such a calyx.

the calyx is in the form of an operculum, under which the stamens are placed as under an arch. At the time of flowering, this calyx gets constricted round the base, and, after being raised by the elasticity of the expanding stamen, drops off. In the North-West American[1] *Eschscholtzia*, now so familiar a plant in European gardens, the calyx is composed of two sepals soldered together by their free extremities, so as to cause it to resemble the extinguisher of a candle. The development of the flower forces up the calyx, by detaching it from its base; it then falls off, and allows the petals to expand. Very similar peculiarities of the calyx to what we find in *Eucalyptus* are seen in other members of the order to which it belongs (Myrtaceæ)—*e.g.*, in *Calyptranthes* of tropical America, *Syzygium* of tropical Asia and Africa, or in the flower-buds of the common clove (*Caryophyllus aromaticus*).

Absence or Presence.—If there are two floral coverings present in a flower, then we may be certain that the outermost one is the calyx; but if the flower possesses but one covering, then opinion is divided whether this should be considered a calyx or a corolla. Thus, in the order Ranunculaceæ, some of the anemones, clematis, &c., noted for their beautiful flowers (*e.g.*, *Clematis lanuginosa*, &c.), owe their beauty to coloured sepals. A whole series of dicotyledonous plants, which Jussieu called *Apetalæ*, have the calyx as the sole floral envelope—*e.g.*, nettles, Chenopodiaceæ, &c. In the Amentaceæ willows (fig. 162), ash (figs. 163, 164), beech, alder, oak, &c., the calyx is even wanting, and is replaced by scales of the nature of bracts. One of the most extraordinary of these is the North American "Dutchman's pipe" (*Aristolochia Sipho*). The calyx forms a "long and thick tube, bent into the form of a siphon, swollen at the base, contracted at the throat and orifice, round which is spread out a limb almost circular, and feebly three-

Figs. 165-170.—Various flowers showing stamens and pistils. Fig. 165.—Naked flower of the ash. Figs. 166 and 167.—Staminiferous and pistillate flowers of the willows. Fig. 168.—Flower of a *Carex* (Sedge), showing the "perigynium" or covering of the pistil, which is borne on a glume. Fig. 169.—Staminiferous flower of the same plant, consisting of a glume, and 3 stamens with innate anthers. Fig. 170.—Spikelet of a grass.

---

[1] California is commonly given as the peculiar country of this species (*E. Californica*). I have, however, seen it growing on the Pemberton Portage in British Columbia, more than seven degrees of latitude north of the Californian boundary line.

lobed" (fig. 171). Duchartre has called attention to the fact that certain Dicotyledons which at first sight seem to possess a corolla outside their coloured petaloid envelope, do not in reality do so. An example of such a plant is afforded by the Marvel of Peru (*Mirabilis Jalapa*). What is usually taken for a calyx is in reality an involucre enclosing a single flower. In *Mirabilis triflora*, Benth.,[1] a similar involucre envelops three flowers; six in *Oxybaphus;* and in *Abronia*, another genus of the same family (Nyctaginaceæ), this calyx-like involucre is situated at the base of a group of numerous flowers.[2]

Fig. 171.—Entire flower of *Aristolochia Sipho*, L'Herit. *ov* Inferior ovary (nat. size).

Use.—The use of the calyx, when present, is most probably for the protection of the more delicate organs within; but when it is entirely absent, or, as in the case of the vine, very minute, we are led to hesitate before bringing the doctrine of "final causes" to bear upon this part of vegetable organism. In many cases, when it remains green, it assists, by performing the function of a leaf, in the nutrition of the plant.

COROLLA.

When the perianth consists of two whorls, then the innermost is called the *corolla* (plural, *corollæ*). This floral envelope, which is usually bright-coloured, and constitutes the most conspicuous part of the flower, is made up of leaf-like organs—equivalent to the sepals of the calyx—called *petals*,[3] each petal being either distinct from the others, or they are coalesced either wholly or in part, so as to constitute one continuous circle, just as we have seen the sepals in many cases are. It is wanting in the apetalous or monochlamydeous Dicotyledons, and most probably in all the Monocotyledons.

Petals.—The petals are leaf-like organs, so far as the shape is concerned, though, as a rule, they are brilliantly coloured. Each petal may be divided into two parts—viz., 1, the *limb*, or expanded upper portion, which is usually coloured; 2, the *unguis*, or claw,

---

[1] *Quamoclidion*, Choisy.

[2] What is sometimes called the *Epicalyx* (επι, upon, *calyx*) on the mallows and other plants, is, in reality, an involucel (fig. 161).

[3] *Petalum* (Latin), from the Greek πέταλον, a coloured leaf.

which is the lower narrowed portion by which the petal is attached to the receptacle. It occasionally happens that the unguis is either imperfectly marked or entirely absent; in this case the petal is *sessile* (Ex. *Ranunculus*). In regular symmetrical corollæ the petals are symmetrical throughout, both as to their own parts and to their neighbours'. In *Helleborus odorus* the five sepals are large and petaloid, while the eight to ten petals are very small, pyramidal in shape, hollow, four-sided, and each with a long claw (*unguiculate*). In *Eranthis hyemalis* (winter aconite) we find a very similar arrangement; while in *Nigella arvensis* (Devil-in-the-bush) the petals are reduced to from five to ten singular, very unpetal-like bodies. In Aconite the petals are represented by two peculiar arched organs; while in the mignonette (*Reseda odorata*) each petal is concave on its internal aspect, while on its external surface is a crest composed of a number of filaments of unequal length crowded together. In Magnolia, *Calycanthus floridus*, and more familiarly in certain species of water-lily, &c., there is a striking transition from the calyx to the corolla, and the converse. Petals, we thus see, are, *morphologically*, only modified leaves; and accordingly, the same terms are used to describe them. Thus petals may be dentate, lobed, crenulate, laciniate, &c. Usually there are in each petal three principal nerves—a median and two lateral ones—but there are variations, which are curiously connected with the mode of insertion of the petals. For instance, if the three nerves enter the claw at the point of insertion separately, then the petal, on falling off, leaves on the receptacle a horse-shoe-shaped mark. On the contrary, if they enter the petal in unison, then the scar left at the place of insertion is rounded.[1] In a gamopetalous corolla the thickened nerves at the lines of union of the margins of contiguous petals point out the number of petals which enter into such a corolla.

Number.—The number of the petals, like that of the sepals, varies. Sometimes they are very numerous, and disposed in a spiral; and more often they are few in number, and arranged in one, two, or a greater number of verticils. If there are two verticils, then the interior one *alternates* with the exterior one—*i.e.*, the petals of the interior verticil are placed in the intervals between the petals of the exterior one. In *Sauvagesia erecta* there is an exception to this rule. Here we find the interior verticil *superimposed* on the exterior one—*i.e.*, its petals lie not on the intervals between, but *on* the petals of the exterior verticil. If there is only a single verticil of petals, then the petals alternate with the sepals in the same manner that the interior verticil alternated with the exterior one. This law also finds an exception. In *Garidella nigellastrum*, and some Ternstrœmiaceæ (*e.g.*, *Tern-*

---

[1] Payer, Eléments, 162.

strœmia peduncularis), the petals are superimposed on the sepals which are placed exactly under them.

Anatomy of the Petals.—As the structure of the sepal was only that of the leaf modified, so in like manner the anatomy of the petal is only a modification of that of the sepal. A delicate epidermis, superiorly and inferiorly, covers a parenchyma made up of loose, large, thin-walled cells, through which ramify the nerves, composed of a few tracheary vessels, which in their ultimate ramification are reduced to a single exceedingly delicate tube. In the petals of some plants—the black henbane (*Hyoscyamus niger*), for instance—the nerves are well marked, and of a purple or other colour, different from that of the rest of the petal. Weiss and others deny that stomata are, as usually stated (p. 54), wanting on petals; and maintain that, on the contrary, though usually very few, examples are not wanting in which they may be found abundantly. If found, they are very indistinctly marked, and confined to the foliaceous petals, or in the coloured ones to the exterior aspect, which corresponds to the under surface of the leaf. On the interior face there are certainly none, and many plants entirely want them. The epidermal cells are often raised in lines or papillæ, which give the velvety appearance to the petals of certain plants, such as the pansy (fig. 33); while throughout the parenchyma of the petals of scented flowers are little reservoirs of the odoriferous essential oil, which are even visible to the naked eye, as in the case of the orange and citron flowers. In a few rare cases, hairs are scattered over the surface of the petals, or they are hollowed into little *fossæ* or pits. On the whole, the substance of the petals is much more delicate than that of the sepals, or other foliar organs of the plant, though they occasionally become fleshy (*Rafflesia*), or hard, stiff, and dry (*Xylopia*, &c).

Corolla, Dialypetalous[1] **and Gamopetalous.**[2]—Like the calyx, the corolla may be dialypetalous or gamopetalous, according as the petals are distinct from each, or are united to a greater or less extent—in the latter case the term used to express the extent of coalescence of the sepals being employed to describe the same characteristics in the corolla. In fig. 172 of the tobacco, we have a gamopetalous corolla; in fig. 173, representing a species of rose, the dialypetalous form.

Dialypetalous Corolla.—In this corolla, the number of petals, like the number of sepals in a dialysepalous calyx, may vary. In the genus *Circæa* (enchanter's nightshade) there are two petals, and the corolla is accordingly called *dipetalous;* in *Cneorum tricoccum* there are three (*tripetalous*); in wallflower four (*tetrapetalous*); in flax and pinks five (*pentapetalous*). In like man-

---

[1] Sometimes called *Polypetalous*.

[2] Sometimes called *Monopetalous*.

ner the terms *hexa- hepta- octo- ennea-* and *deca-petalous* are used to express the presence of six, seven, eight, nine, and ten petals in a corolla, though in general, when there are more than five, the word *polypetalous* is used. Though the petals are to all intents and purposes leaves, yet in the dialypetalous corolla there are some peculiar forms, as witness the Aconite and Hellebore, already noticed, or *Delphinium*, in which (as in *D. Ajacis*, the common larkspur) the petals are two combined into one,—this single petal being lengthened into a spur within that of the calyx—this calycine spur being often as long as the rest of the flower. The petals may be also straight, inflexed (as in Umbelliferæ, fig. 174), reflexed, &c.; and, like the sepals, their arrangement and symmetry, or the want of it, may give rise to a *regular* or *irregular* corolla—the various forms of flowers which Tournefort took as the basis of his classification of plants being dependent on the arrangement and form of the petals.

Fig. 172. — Entire expanded flower of Tobacco (*Nicotiana Tabacum*, L.) *s* Calyx; *c* Tube of corolla; *c'* Throat; *c''* Limb (nat. size).

Fig. 173.—Open flower of *Rosa arvensis*, Huds. *c c c c c* The five petals of the corolla; *e* The numerous stamens; *p* The pistil; *pd* The peduncle or support of the flower.

Fig. 174.—Flower of the common Fennel (*Fœniculum vulgare*, Gærtn.), showing the incurved petals, owing to the strongly-marked median line being prolonged to the apex of each petal. This line forms a ridge interiorly, a furrow exteriorly (5 times nat. size).

A. *Regular Dialypetalous Corolla.*—Under this head we may notice three chief forms of corolla. 1. The *cruciform* corolla (fig. 182), in which there are four petals, arranged in the form of a Greek cross. *Ex.* Wallflower and the other members of the whole order Cruciferæ. 2. *Rosaceous* (fig. 187), in which there are five and sometimes four large, very short-clawed petals spread out in a circle. *Ex.*

Rose, strawberry, cherry, and other members of the order Rosaceæ. It is the form of corolla which occurs most frequently among dialypetalous corollas. 3. *Caryophyllaceous*, in which there are five long-clawed petals attached to the bottom of a tubular or gamosepalous calyx. *Ex.* Pink, and the other members of the order Caryophyllaceæ (fig. 183). 4. *Liliaceous*, characteristics of the lilies. Here we find the claws of the segments of the perianth erect, and gradually spreading towards their summits.

Figs. 175-187.—Various forms of calyx and corolla.

B. *Irregular Dialypetalous Corolla.*—One of the most remarkable is the *Papilionaceous* or Butterfly[1] corolla, so called from its resemblance to that insect. It is characteristic of the *Papilionaceæ* or *Leguminosæ*, the order to which peas, beans, vetches, whin, &c., belong. The corolla of any of these plants will show the following arrangement of the petals (figs. 188, 189, 190): 1. Superiorly is an undivided petal, generally larger than the others, called the *vexillum* or standard. 2. At the sides are two others of equal size and

---

[1] *Papilio*, a butterfly.

shape, called the *alæ* or wings. 3. Lastly, inferiorly are two others, symmetrical in form and size, which are often coalesced the one with the other, either in part, or, as in fig. 185, D, altogether by their inferior border, in the form of a boat, or of a vessel with a keel—hence called the *carina* or keel of the papilionaceous corolla. In the common haricot (*Phaseolus vulgaris*), the keel is curiously twisted into a spiral form like a snail's shell. In *Trifolium resupinatum*, the positions of the parts mentioned are inverted—the standard being at the lower and the keel at the upper part of the corolla. In *Amorpha* we find both keel and wings have disappeared, leaving the corolla unipetalous. This is occasionally seen as an abnormality in other Leguminosæ. Hence Moquin-Tandon considered that the *standard* was the only petal "normal and regular to the papilionaceous corolla." In the keel of Leguminosæ the stamens and petals are placed.

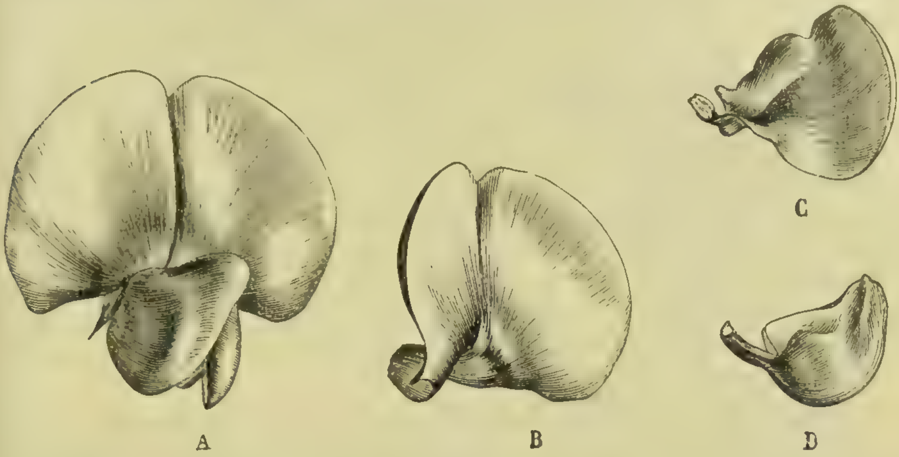


Fig. 188.—Flower of a leguminous plant (*Lathyrus latifolius*). A, Entire and in portion; B, The vexillum or standard; C, One of the alæ or wings; D, The carina or keel.

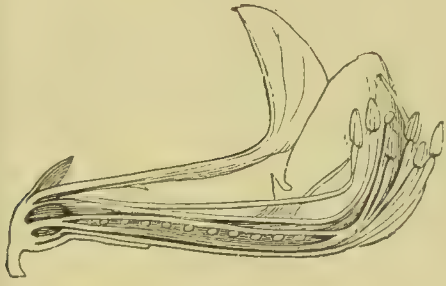


Fig. 189.—Longitudinal section (magnified) of the flower of a leguminous plant of the genus *Coronilla*.

Fig. 190.—Diagram of the flower of *Tetragonolobus*, one of the Leguminosæ.

Under the term *anomalæ* are sometimes classed a variety of forms of corolla which cannot be conveniently placed under any of the foregoing heads. Among these may be mentioned the corolla of the mignonette, which we have already had occasion to refer to, and that of the garden balsam (*Balsamina hortensis*), *Lopezia racemosa*, *Polygala vulgaris* (milkwort), and *Pelargonium grandiflorum*. Our space will only permit us to notice that of *Lopezia*. Here we have a calyx of four sepals which present nothing abnormal; the corolla is made up of four petals, of which two are large with oval limbs, while the other two are small, narrow, bent at a third part of their length, with a swelling at the "knee:" finally, there is a third little petal remarkable for its elastic claw, which is bent and hollow. This petal M. Duchartre, however, sees good reason for considering only a stamen transformed and petalised.

Gamopetalous Corolla.—Here the petals may, like the sepals in the gamosepalous calyx, be either coalesced by their entire length, or only by a part. Hence, like the calyx of a similar nature, the same terms used to describe the margin of leaves are applied to describe the extent of union of the petals in this kind of corolla—the gamopetalous corolla being looked upon for the sake of convenience, like the gamosepalous calyx, as a single organ. We might, however, remember that in both cases we are not dealing with a single organ, but with several in union; and that the spaces left between the non-coalesced sepals or petals are of an entirely different nature in their origin from the divisions in the margins of leaves. It is unnecessary to repeat these terms, which are the same as for the leaves or the sepals (fig. 191). As in the gamosepalous calyx, there may in the gamopetalous corolla be distinguished,—1, the *tube*; 2, *limb*; 3, *throat*. The form or character of these parts is used in describing the forms of corolla. Thus the tube may be *long*, *swollen*, *cylindrical*, *angular*, &c.; the limb *plain* or *concave*, with 2, 3, 4, or 5 lobes or segments; the lobes being in their turn *obtuse*, *oval*, *rounded*, *lanceolate*, *cordate*, &c.; while the *throat* may be bare or furnished with hairs, glands, and appendages of different kinds.

Fig. 191. — Flower of Pimpernel (*Anagallis arvensis*), with a quinquepartite corolla *c*; *s* Calyx.

Scales (*squamæ*, *fornices*).—Though in reality in the majority of cases there is no marked distinction between the throat and the tube, yet it is in the throat where most frequently are found the various appendages of the interior of the corolla—such as the tufts of hairs, the prominences known as scales, &c. Thus, in *Samolus Valerandi* (the common brookweed) we find scales which some botanists look upon as imperfectly-developed stamens (fig. 192, *e'*).

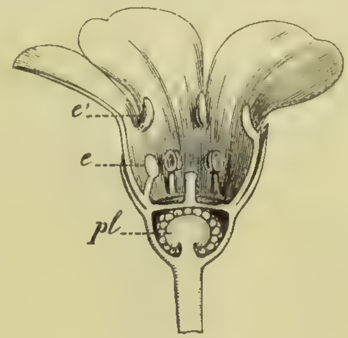


Fig. 192.—Flower of Brookweed (*Samolus Valerandi*) in longitudinal section. *e'* Scales; *e* Developed stamens; *pl* Placenta, with ovules.

Other Appendages of Corolla.—In the genus *Silene* (and notably in *Silene pendula*), and many other Caryophyllaceæ, at the inner side of the point where the limb of each petal meets the claw, there is a little (usually two-lobed) upward projection or *lamella*, generally twisted, as if the claw was continued in this direction. The result is that, when the petals are all in position in the corolla, there is a *corona* or crown round the orifice of the tube formed by the five lamellæ in union. Something similar is seen in the oleander (*Nerium Oleander*)—in this case the corona being formed by a series of fringed lamellæ attached to the petals. In the *Narcissus poeticus*, and still more markedly in the "hoop-petticoat" species (*N. Bulbocodium*), there is a corona composed of a single piece; but whether this is to be looked upon merely as an appendage to the corolla, or as identical with the scales (p. 312) already spoken of, is still a subject of dispute among botanists who have made a study of the morphology of these organs. The scales in the borages[1] (fig. 194), the appendages we have already spoken of as existing on the petals of *Lychnis*, *Silene* (at the line of junction of the limb and the claw), and the petaloid bands fixed on the lateral nerves of the five petals of the corolla of *Hydrophyllum* and *Phacelia*, are considered by Payer to be also of this nature.

Union of Stamens with Corolla.—We shall have occasion, while in the next chapter speaking of the andrœcium, to describe the connection of the stamens with the different parts of the perianth. In the mean time, we may mention that, as a rule, the stamens in the gamopetalous corolla are *attached* to the corolla, or in other form have their extremities so blended with the substance of the corolla as to seem to rise out of it (fig. 193). To this rule there are, however, exceptions. For instance, in the order Plumbaginaceæ, the corolla in the genus *Plumbago* (leadwort) is gamopetalous, but the stamens are not attached to it; while in the sea-pink (*Armeria*) and sea-lavender (*Statice*) the five petals are united at their base only to a small extent, and the stamens have only a slight connection with them, and then only at the point of union

---

[1] All the European species, *Echium* and *Pulmonaria* excepted.

of the claws. In the whole heath order (Ericaceæ) the stamens are also independent of the corolla.

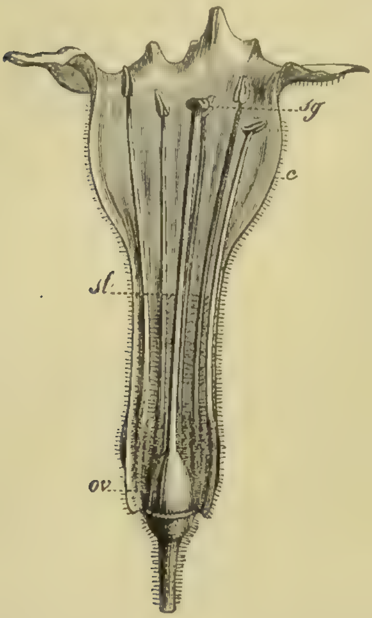


Fig. 193.—Flower of the Tobacco (*Nicotiana Tabacum*, L.) opened. *c* Corolla; *ov* Ovary; *st* Style; *sg* Stigma.

Let us now examine briefly a few of the more marked forms of gamopetalous corollas. Like the dialypetalous corolla, the gamopetalous one may be regular or irregular, and from identical causes to those which render the gamosepalous calyx regular or irregular.

A. *Regular Gamopetalous Corolla.*—This class is rather more varied in forms than the corresponding dialypetalous corolla. For instance, the following forms are well marked: 1. The *Campanulate* or bell-shaped corolla (fig. 184). *Ex.* Harebell (*Campanula*), *Convolvulus*, &c. 2. *Infundibuliform* or funnel-shaped (fig. 169). *Ex.* Tobacco. 3. *Hypocrateriform* (or hypocraterimorphous) or salver-shaped. *Ex.* Primrose, Syringa, Jasmine (fig. 181). 4. *Rotate* or wheel-shaped. *Ex.* Forget-me-not (*Myosotis*) and potato (fig. 180). 5. *Stellate* or star-shaped is perhaps only a modification of the rotate form. Ex. *Galium* or bed-straw, or the common Borage (*Borago officinalis*) (fig. 194). 6. *Globose* or globe-shaped (urn-shaped), of which the terms *ovoid* and *urceolate* are only modifications. Examples of all these shapes may be found in the different species of heath (fig. 176). 7. Lastly, we may note the *tubular* corolla, seen in the inner flowers of the *capitula* or heads of flower of Compositæ, such as the thistle, dandelion, daisy, &c. (figs. 195 *a*, 178, 179).

Fig. 194.—Flower of the common Borage (*Borago officinalis*, L.), with stellate corolla; *éc* Five scales at throat; *e* Stamens.

B. *Irregular Gamopetalous Corolla.*—The forms of this class are much less numerous, but are more clearly marked, than the preceding ones. We may distinguish the following: 1. The *Labiate* or lipped corolla, distinctive of the whole order Labiatæ, "when in a four or five lipped corolla the two or three upper lobes stand obviously up like an *upper lip*[1] from the two or three lower ones or *under*

---

[1] Sometimes called the *galea* or helmet.

lip."[1] When, as in the dead-nettle (*Lamium*), bugle (*Ajuga*), and most of the common *Labiatæ* (fig. 177), the two lips of the corolla are wide apart, the corolla is said to be *ringent* (grinning) or *unilabiate* (one-lipped, the upper one being out of all proportion to the lower one); while if, as in the snapdragon (*Antirrhinum*), they are in contact, or closed by a projection from the base of one of them called a *palate*, the term personate (masked) or *bilabiate* (two-lipped) is applied to the corolla (fig. 175). In the snapdragon the base of the corolla is somewhat protuberant or *saccate* (fig. 186), and in the toadflax (*Linaria*) this protuberance extends into a spur, which is common in various orders (*e.g.*, violet, fumitory, &c.); while in the larkspur the whole five petals are thus calcarate or spurred.

In the toadflax is occasionally a monstrosity, in which not only one, but the whole five petals of the corolla are thus spurred. In 1742, Linnæus found such a plant near Upsal, and was so astonished at the monstrosity exhibited by it, which he considered due to an accidental fecundation by another plant, that he called it by the name *peloria*.[2] The name is now applied to this kind of monstrosity in different flowers, and in the case of irregular flowers like the toadflax, may be looked upon as an effort of the plant to bring back the flower "to a singular abnormal state of regularity."

2. The *ligulate* flowers of the exterior part of the heads or "*capitula* of composite" plants like the dandelion, chicory, daisy, &c. In the interior of the inflorescence of these plants, we find tubular flowers (fig. 192, *a*); but towards the circumference the flowers are irregular in shape, one side of the corolla being prolonged into a *ligula* or strap-shaped form (fig. 195 *b*).[3]

Fig. 195.—Ligulate (*b*) and tubular (*a*) flowers of a composite plant.

Finally, there are forms of corolla which it is impossible to class under any of the divisions given, and which have therefore received the somewhat vague title of *anomalæ*. Among these anomalous corollæ is that of the folks-glove (*Digitalis purpurea*), which is shaped

---

[1] Sometimes called the *labellum*, though this term is usually reserved for one of the divisions of the perianth in *Orchidaceæ* and a few other orders.

[2] πέλωρ, monster (Amœn. Acad., i. 55, t. iii. 1 (1744).

[3] Sometimes, especially by the French botanists, the term *flosculus* (fleuron) is given to the tubular flowers, and *semi-flosculus* (demi-fleuron) to the ligulate ones.

like the finger of a glove — hence the name. Such a form of corolla is sometimes called *digitatiform*. Among other peculiar ones may be mentioned the corollas of the mullein (*Verbascum*), the *Veronica* or speedwell, the *Lobelia*, the *Stylidium*, &c.

We find the corolla, like the calyx, not always equally developed in all the flowers of the same inflorescence. A marked example of this we have already had occasion to notice in the Compositæ, where the inner flowers are regular, tubular, and quinquedentate; while the marginal ones are irregular, one part of the corolla being much developed in the strap-shaped prolongation characteristic of these ligulate flowers. An identical arrangement is seen in the *Dahlia*.

Colour of Corolla.—The calyx is usually green, while this colour is only exceptionally found—as in *Hoya viridiflora*, *Genolobus viridiflorus*, &c.—in the corolla. Black is a colour which really does not obtain in the corolla, what is usually so called[1] being only a purple-red, blue, or deep brown; while, as a rule, the colours of the corolla are of a gay character, or are blended together in that inimitable manner which gives the beautiful variety to flowers. This subject we will have occasion again to refer to more in detail—(SECTION IV.)

Duration of the Corolla. — Corollas, like calyces, may be classed according to their duration, as *caducous*, *deciduous*, and *marcescent*. In the first case, the corolla falls off soon after the opening of the flowers (Ex., *Papaver Argemone*, flax, various species of *Cistus*, *Cereus*, &c.); in the second, which is by far the most common case, the corolla falls after the fecundation of the ovules or young seeds; while in the last division the corolla remains in a faded condition after the process of fecundation has been completed and the fruit has commenced to mature (*Ex.*, some species of *Erica* or heath, various *Cucurbitaceæ* (gourds), &c.

In the greater number of flowers, however, no sooner have the anthers discharged their pollen on the stigma, and the pollen-tubes penetrated through the tissue of the pistil to the ovules, than the corolla begins to fade, and soon after drops off. This is the reason why double flowers, in which the essential reproductive organs have been transformed into petals, last longer than single flowers.

Use of Corolla.—Though in general the floral envelope which most prominently attracts the eye, the corolla is probably, physiologically, the least important of the floral whorls. It is in general too delicate to serve as a protection to the essential organs within it, unless, indeed, as in the vine, the calyx is so small that it has to supply its place in this respect. There is, however, little doubt

---

[1] For example, in *Pelargonium tricolor* and *Vicia Faba*.

that when it secretes honey or other sugary liquid at the bottom of the tube, by attracting insects to it—which, in their turn, convey the pollen from flower to flower—it serves a highly important purpose in the economy of nature. This subject has of late years attracted so much attention that we shall, at the proper place, enter into a somewhat full outline of the recent researches on this question of the use of the corolla—(Chap. IX.)

PERIANTH OF MONOCOTYLEDONS.

The perianth of Monocotyledons, when they possess any floral envelopes, differs very considerably from that of Dicotyledons. Usually the segments of it are three in number, or some multiple of three—very commonly six—and are often gaily coloured, as in the tulips, lilies, &c. When the latter number are present—as in a tulip, for instance—the petals are arranged in two whorls. The question now arises, Is the exterior whorl a calyx, and the interior one a corolla? The older botanists, whenever they saw a covering exterior and green, called it a calyx; but we now know that colour is no test whatever of the nature of the perianth. The greater number of modern botanists, from a study of the nature of this perianth in Monocotyledons, and from the fact that, as a rule, the segments of it do not alternate with the whorl of stamens, have concluded that it is not a corolla, but a calyx; and that even when more than one whorl is present, the position, nature, and coloration of the segments, and their tendency to unite by their base to form a single tube, still lead us to look upon the monocotyledonous perianth as a calyx in two whorls.[1] It ought not, however, to be denied that some eminent botanists are inclined to allow two coverings, and point out that in some plants the position and coloration of the two whorls give ground to this belief in two series of floral envelopes being present in at least some Monocotyledons. For instance, in the Virginian day-flower[2] (*Commelyna Virginica*), and other species of the order Commelynaceæ and Alismaceæ, the three exterior segments of the perianth are foliaceous, and have all the characters of a calyx; while the three interior ones are larger, more delicate, and are brightly coloured, thus presenting all the characters of a calyx. In *Alisma Plantago*

---

[1] In the *Iridaceæ* and other orders we find the stamens inserted on the coloured organ which we consider a calyx,—a startling proof that it is really so; for though we often find the stamens united with the corolla, yet never do we find them *inserted* on that floral envelope, but either on the receptacle, like the petals, or on the calyx.

[2] So called because the flowers expand for a single morning, and are recurved on the pedicel before and after that period.

(water-plantain) we find the same characteristics in the perianth. Opinion being so equally divided, De Candolle proposed to style the floral envelope of Monocotyledons the *Perigonium*[1] — an unnecessary term, as the phrase *single or double perianth* equally expresses its character, without committing ourselves to an opinion regarding its nature.

In Orchidaceæ the flower is very irregular. The perianth is composed of six segments in two sets—an exterior and an interior one—both sets being, however, of the same texture and petal-like appearance. The upper or posterior segment of the interior whorl (but which, by the twisting of the ovary or stalk, commonly appears the lower or anterior one) differs in shape and direction from the others, being often spurred and appendaged, and is called the *labellum* or lip. In *Paxtonia* and *Isochilus* the labellum does not, however, differ from the other segments of the perianth. The structure of the perianth of orchids is, however, so intimately connected with the very peculiar structure of the whole of the flower, that I consider it would be more instructive to the student to reserve the description of it until we have occasion to notice the extraordinary mode of fertilisation prevailing in the order—(Chap. IX.) In *Zingiberaceæ* and *Cannaceæ* (or Marantaceæ) there is also a labellum ; but this is not a part of the perianth proper, but appears to result from transformed and reunited stamens, on which account Lestiboudois has given the name *Synema* to it.

---

[1] The segments being called *Tepals.*

CHAPTER III.

THE ANDRŒCIUM,[1] OR STAMINAL WHORL.

THIS constitutes the third whorl, and in a perfect flower is placed next to the corolla. It is made up of *stamens*, which are either free, or variously united among themselves or to other floral organs. They develop the *pollen* cells or grains by means of which the young seeds or *ovules* are fertilised, so as to be enabled to produce the *embryo* or young plant within the seed. The stamens are thus organs essential to the reproduction of the species.

STAMENS.

A stamen[2] is made up of the *filament* and the *anther*—in other words, of a stalk and a head (fig. 196). The anther is composed of two sacs or *thecæ*, which contain the *pollen*. This pollen is a dust-like substance, which, on microscopic examination, is found to consist of a multitude of either single cells or of several cells in combination. Finally, the filament is generally long and slender, supporting the anther, though sometimes it is wanting, in which case the anther is *sessile*.

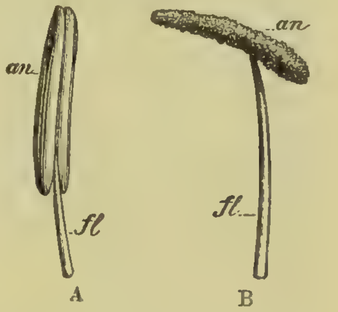


Fig. 196.—Stamens of *Lilium superbum*, L. A, *an* The anther, ready to discharge the pollen; *fl* Filament. B, *an* The same anther opened and completely emptied of pollen, and so almost horizontally placed in the filament *fl*.

Number of Stamens.—The number of the stamens varies from one to a great number. From the number of the stamens Linnæus, in the celebrated classification of plants which bears his name, formed the first eleven or twelve classes; and the terms which he

---

[1] Or *androcium* (Röper), from ἀνηρ, a man or male, and οἶκος, a habitation; it is sometimes spelt *andrœcium*. The stamens were the "chives" or "capillimenta" of the older botanists, who named the anthers *apices* (Blair's Botanik Essays, p. 29, 1720); but as late as 1682, Grew styled the andrœcium "the seminiform attire," while the perianth was "the florid attire."—Anatomy of Plants, p. 171.

[2] *Stamen*, a thread.

applied to these classes are still retained in descriptive botany to express the number of members of the staminal whorl. Thus, when there is only one stamen, the plant is *monandrous*,[1]—*Ex.* the mare's-tail (*Hippuris vulgaris*); when two (*veronica*) *diandrous*;[2] three, *triandrous*[3] (Iris, grasses); *tetrandrous*[4] when four (*Delphinium*); *pentandrous*[5] when five (*Aquilegia*); *hexandrous*[6] when six (lily, tulip); *heptandrous*[7] when seven (horse-chestnut); *octandrous*[8] when eight (heaths); *enneandrous*[9] when nine (rhubarb, laurel); *decandrous*[10] when ten (saxifrages); *dodecandrous*[11] when twelve (*Asarum*). When there are more than twelve, and up to twenty, and the stamens are inserted on the calyx, the term *isocandrous*[12] (*Ex.* Mignonette) is applied; when they are inserted on the receptacle, and are more than twenty, then the stamens are said to be *polyandrous*[13] (*Ex.* Poppy, Ranunculus, &c.) If below twelve in number, the general term *definite*[14] is frequently applied to them; but if more than twelve in number, they are vaguely said to be *indefinite*, and are indicated by the sign ∞. The stamens may either be the same as, or different in number from, the other whorls of the flower, particularly the corolla. For example, in the vine, carrot, *Erodium* ("heron's bill"), the number of the stamens is the same as the number of the divisions of a gamopetalous corolla or *Isostemonous*[15]. On the other hand, they may be *Anistemonous*,[16] or different in number from the divisions of the corolla. These anistemonous stamens resolve themselves into two divisions—viz.: (*a*) Those which are *meiostemonous*,[17] or less in number than the petals; and (*β*) those which are *polystemonous*,[18] or more than the petals in number. The *Pelargonium* supplies an example of the first, while the *Geranium* is an example of the second case. In the Geranium the stamens are exactly double the number of petals, or *Diplostemonous*.[19] Finally, to show what variety exists in these relations of the stamen, it may be mentioned that all these three numerical varieties may, and frequently do, occur in one order. It may occasionally happen, as a teratological change, that all the stamens in a hermaphrodite flower are suppressed (*Meiotaxy*); while of course this occurs naturally in a pistilline flower. There may, on the other hand, not only be an increase in the number of stamens, but an increase in the number of whorls, especially in

---

[1] *μονος*, one; *ἀνηρ*, man.
[2] *δύο*, two.
[3] *τρεῖς*, *τρια*, three.
[4] *τέτρα*, four.
[5] *πέντε*, five.
[6] *ἕξ*, six.
[7] *ἑπτά*, seven.
[8] *ὀκτω*, eight.
[9] *ἐννέα*, nine,
[10] *δέκα*, ten.
[11] *δώδεκα*, twelve.
[12] *ἕικοσοι*, twenty.
[13] *πολυς*, many.

[14] In this case the flower is sometimes styled *oligandrous* (ὀλίγος, few), and in descriptive writings is marked by the sign °°.

[15] *ἵσος*, equal; and *στήμων*, a stamen.
[16] *ἄνισος*, unequal.
[17] *μείων*, less.
[18] *πολυς*, many.
[19] *διπλόος*, double.

cases where the number of the circles of stamens is naturally large (this constituting *Pleiotaxy*). Lastly, Dr Masters notes that an increase in the number of the stamens frequently accompanies a corresponding alteration in the other whorls.

Relative lengths of the Stamens.—All the stamens in a flower may not be of the same length—some being long, while others are short. In some cases there is almost a regularity in this, as in *Oxalis* (sorrel), where the ten stamens are alternately longer and shorter. On the basis of the relative lengths of the stamens, Linnæus founded two of his classes; and the names he applied to these classes are still used to designate the peculiarity in the staminal whorl which suggested the designations. Thus, when a flower contains four stamens, two of which are evidently shorter than the others, it is styled *didynamous*.[1] Nearly all the thyme and dead-nettle order (Labiatæ), the toadflax (*Linaria vulgaris*), the snapdragon (*Antirrhinum*), and most of the Scrophulariaceæ (fig. 200), are of this nature. On the contrary, when there are six stamens on the flower, of which four are longer than the other two, the term *tetradynamous*[2] is given to this variation. The whole order Cruciferæ (wallflower, &c.) is distinguished by this among other characters.

Among plants with five petals and ten stamens (*e.g.*, *Dianthus*, *Silene*, &c.), five of the stamens are placed opposite to the petals, and differ much in length from the other five in the second whorl, which are alternate with the petals. Finally, in some flowers, like the lily, tulip, &c., the stamens are all of equal length. This subject of the relative lengths of the stamen has of late years assumed great importance, from the interesting observations of Darwin in regard to the different fertilising powers which the long and short stamened flowers of the primroses, &c., possess. This subject of dimorphic and trimorphic plants we shall have occasion to speak about at greater length when discussing the various modes in which plants are fertilised (Chap. IX.)

197.

198.

199.

200.

Figs. 197-200.—Showing modes of union, &c., of stamens.

Regularity and Irregularity of the Andrœcium.—Like the calyx and corolla, the staminal whorl may be regular or irregular.

---

[1] δύο, two; δυναμις, greatness.

[2] τέτρα, four.

Thus it is *regular* when all the stamens are of the same length, and inserted on the receptacle at the same height and at equal distances; when the contrary is the case, then it is *irregular*, unless, indeed, these irregularities follow some uniform law. Thus, in the white water-lily (*Nymphæa alba*), the stamens being in a spiral, are inserted gradually nearer and nearer the centre: they are also gradually smaller and smaller, and the distance which separates them varies; yet the andrœcium is still regular, because these irregularities of size, insertion, and distance follow a uniform law.[1]

Situation in regard to Petals and Sepals.—When there is only one whorl to the andrœcium, the stamens are generally alternate with the segments of a gamopetalous corolla—or with the petals of a dialypetalous one, when equal in number to the segments or petals (*e.g.*, borages, Umbelliferæ, &c.) In some cases the stamens are opposite to the petals, as in the primrose, vine, Plumbaginaceæ (sea-pink order), &c. In such a case we are justified in concluding, from our knowledge of the plan of the flower, that either one whorl of petals is suppressed, or, as in the case of Monocotyledons, only the calyx is present. Again, when, as in Silene, we find the number of stamens ten, while the petals are only five; the stamens, though seemingly of only one whorl, are looked upon as consisting of two. The other causes which lead to such apparent irregularity in the arrangement of the floral organ we shall in due course consider somewhat more in detail (Chap. V.)

Adhesion.—They may be all distinct and free, or adhere to each other either by the filaments or anthers, or by both. In other cases they may be "inserted" on the sepals, or united to the petals, as in all cases where the simple perianth is gamosepalous, or where the corolla is gamopetalous (*Ex.*, hyacinth, *Daphne*, in which they are inserted on the calyx, and Campanulaceæ, Labiatæ, &c., in which they are attached to the corolla). The stamens may even be united to the carpels—*e.g.*, in the case of the Aristolochiaceæ and orchids, as we shall have occasion to describe when speaking of the anther and filament.

Let us now consider each of the parts of a stamen more in detail.

Filament.[2]—This, when present, forms the stalk or support of the anther. It varies in form and dimension, and is usually colourless, though in some cases, both in form and bright colour, it simulates the petals. In some cases (grasses) it is *capillary* or hair-like, or thick, cylindrical, and dilated at the base, as in *Ornithogalum Arabicum* or *O. Pyrenaïcum*. In the white water-lily,

---

[1] Payer, l. c., 186.

[2] *Capillimentum* or *pediculus*; *filamentum*—from *filum*, a thread.

Canna, &c., it is *petaloid* (fig. 201); in *Dianella cærulea* (fig. 211), ribbon-like; and in *Lopezia racemosa* (fig. 202) it is excavated, so as to have a groove or gutter down its entire length. In *Thalictrum*, *Nerium Oleander* (fig. 208), &c., it is *clavate* or club-shaped; in *Mahernia*, &c., geniculate or kneed (fig. 211); in *Crambe*, bifurcate; in *Anthericum*, bearded or stupose, &c. But in general it is rather subulate or tapering in form (fig. 202).

Fig. 201.—Stamen and style of *Canna pedunculata*, Lodd. *e* The anther; *fl* Its petaloid filament; *p* Style flattened into a petaloid lamina.

Fig. 202.—Stamen of *Lopezia racemosa*, with an ovoid anther and the filament grooved and subulate at its summit.

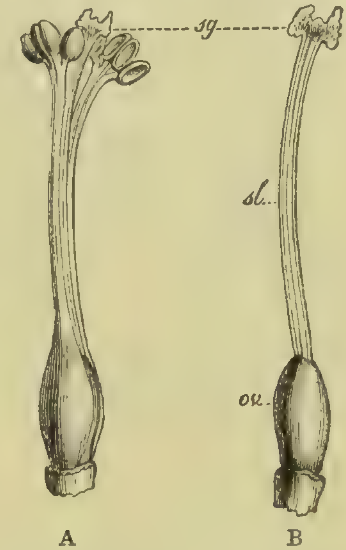


Fig. 203.—Reproductive organs of Fumitory (*Fumaria officinalis*, L.) A, General view, showing the two bundles of stamens surrounding the pistil; B, The pistil isolated; *ov* Ovary; *sl* Style; *sg* Stigma.

Appendages.—In a few cases the filament is enlarged at the base, and presents on each side a small ear-shaped appendage, which some morphologists look upon as representing the sheath of a leaf (as in the asphodel). In the borage and other plants, the filament appears to give rise, either at some distance from the base or at the base itself, to a little lamella-like appendage, the exact morphology of which is not very clearly made out.

Union.—Each filament in an andrœcium may be either perfectly free, or united, either by the whole or a part of its length, to the others, so as to give rise to one or more bundles—"brotherhoods," or *adelphiæ*—of stamens in a single flower.[1] 1. If the filaments are so coalesced as to form one single bundle in the

---

[1] The tube formed by the union of the filaments of monodelphous stems has been called *androphores* (male-bearer—ἀνήρ, and φορέω, I bear) or *phalanges* (fingers). Endlicher styled each of them a *synema*; but this term we have already used in a different sense.

form of a tube (fig. 199), then the stamens are said to be *Monodelphous*[1]—Ex., *Lysimachia vulgaris* (loosestrife), lupines, flax, most Malvaceæ, &c. 2. If the filaments are united so as to divide the stamens into two bundles, as in the fumitory, beans, &c., then they are *Diadelphous*[2] (figs. 197, 204). (*a*) The bundles may be either composed of an equal number of stamens (as in the fumitory, fig. 203, where there are three in each bundle—or in the milkwort, where four is the number), or (*b*) they may be unequal in number, as in the haricots and some Leguminosæ, where one of the bundles is made up of nine stamens and the other of one (fig. 197). 3. When there are three or a greater number of bundles, the stamens are said to be *Polydelphous*.[3] Or they are more accurately termed *Triadelphous*, if, as in the St John's wort (*Hypericum*), they are three in number (fig. 198); *Pentadelphous*, if, as in *Melaleuca*, they are five; and so on. In the castor-oil plant (*Ricinus*) the "androphores" are numerous and unequal in the number of stamens in each.

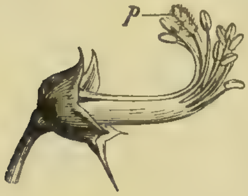


Fig. 204.—Calyx and reproductive organs of *Lathyrus latifolius*, L., ten diadelphous stamens; *p* Extremity of pistil.

When the androphores are the same in number as the petals, then they are always opposite to them, as in *Beaufortia*, *Melaleuca*, &c.

Anthers.[4]—This is the only essential part of the stamen, containing and developing, as it does, the pollen, which is the fecundating principle of the seed. It is usually made up of two lobes or pouches, called *Thecæ*,[5] attached to each other either by their sides, or by the aid of an intermediate body called the *connective*.[6] Each of these thecæ opens at the proper season, and discharges the pollen which has developed in its interior. There are generally two lobes, in which case the anther is styled *bilocular*[7] (*i.e.*, with two *loculi* or pouches). Such an anther is shown on transverse section in fig. 205. The anther has just opened; the connective, through which the vascular bundle goes, is shown at *fv;* and right and left of this we see the two thecæ *a*. At an earlier stage of the anther each of these thecæ was divided into other two by a partition, which gets absorbed in the course of growth, but the former existence of which is shown by the furrow on the wall where it

---

[1] μονος, one; ἀδελφός, brother. [2] δυό, two. [3] πολυς, many.

[4] *Theca* (Grew), *Testiculus* or *Testis* (Vaillant), Spermatocystidum (Hedwig). *Capsula* (Malpighi); *anthera*, from ανθηρὸς (Smith), belonging to the flower.

[5] *Loculi* or *coniothecæ* of some botanists.

[6] *Connectere*, to join.

[7] Sometimes terms of Greek origin are used instead, and the anthers are described as *mono- di- tri-* and *tetra- thecal.*

has opened at *a*. In a few instances there is only one theca (as in all true mallows, Epicradaceæ, Polygalaceæ, &c.), and consequently no connective. In those anthers there were originally two thecæ, but one has become abortive. On the other hand, some anthers are *quadrilocular*, or with four thecæ — *e.g.*, some laurels, the flowering rush (*Butomus umbellatus*), the joint fir (*Ephedra altissima*), the genus *Tetratheca*, the cinnamon plant (*Cinnamonum Zeylanicum*, fig. 206), &c.[1] In the anthers of the mistletoe (*Viscum*), *Rafflesia*, numerous thecæ have been described. Lastly, in the genus *Pachystemnon*, one of the Euphorbiaceæ, the anther is *trilocular*, or possessed of three thecæ.

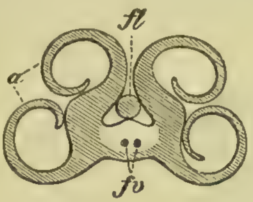


Fig. 205. — Transverse section of the anther of *Lilium superbum*, two of the thecæ of which have already opened to allow of the pollen escaping. *a* Lateral line where the thecæ open; *fv* Vascular bundles which penetrate the connective; *fl* Transverse section of the filament, the top of which is inserted at the bottom of the longitudinal furrow between the thecæ.

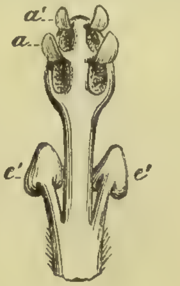


Fig. 206.—Stamen of the Cinnamon plant (*Cinnamonum Zeylanicum*, Breyn.), with quadrilocular anther, and at the base two imperfect stamens *e' e'*; *a' a'* Valves by which the thecæ dehisce.

Shape.—The shape of the anther is very variable. It is generally more or less elongated, but sometimes *ovoid* or ellipsoid (fig. 202), *globular*, *cordiform*, *linear*, *reniform*, *sagittate*, *oblong* (fig. 193), &c. In some Umbelliferæ the anther is broader than long (didymous). The summit of the anther may terminate variously. For instance, it is acute in the borage (*Borago officinalis*); *bifid* or cleft either at its base or summit, as in many grasses; *bicorn* (terminating in two horn-like points) in heath, the arbutus, &c.; or *quadricorn*, as in the case of the *Gaultheria*, one of the heath order belonging to America.

Appendages of the Anther.—These are derived from the connective, and are seen in the anthers of the stamens of many Compositæ in the form of terminal prolongations of the connective above the apex of the anther. In various of the violets we also see appendages, though of a different nature to that mentioned. They are figured in the accompanying illustration (fig. 207) in the shape of a long *queue* formed of a prolongation of the connective of two anthers. In the Oleander (*Nerium Oleander*) the anther is borne on a filament club-shaped at its upper end, along either side of which hang the two lobes in the form of horns, while the

---

[1] According to Schleiden, there are more than a hundred families (grasses, sedges, lilies, Labiatæ, Boraginaceæ, Scrophulariaceæ, Compositæ, Umbelliferæ, Ranunculaceæ, Leguminosæ, Rosaceæ) in which the anthers are quadrilocular before bursting.

connective is prolonged superiorly into a long cord bristling with hairs, and obtuse, and somewhat thicker at its extremity (fig. 208). In *Borage* the appendix is *corniculate* (fig. 209).

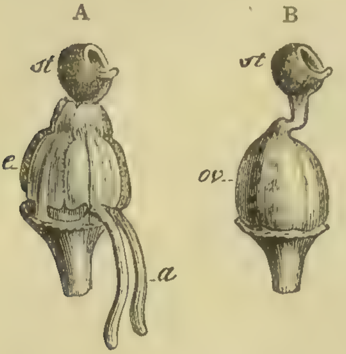


Fig. 207.—Reproductive organs of *Viola tricolor*, L., var. *alpestris*. A, General view; *e* The five stamens, with very short filament, and the anther furnished with a terminal appendix, the two upper ones presenting a long basilar appendage, *a*, of the connective; *st* Extremities of the pistil. B, Pistil detached; *ov* Ovary; *st* Stigma.

Position of the Anther, &c.—Each anther is divided longitudinally by a furrow formed by the two converging sides of the thecæ. The *face* of the anther is that side where the furrow is placed; the *back* is the opposite part; while the *base* is the inferior and the *apex* the superior point, or that exactly opposite to the base.

When the face of the anther is turned to the centre of the flower it is *introrse*,[1] as in wallflower, Iridaceæ, many Ranunculaceæ, Buttneriaceæ, &c. (fig. 210); when, as less commonly happens, it is turned to the exterior, it is *extrorse*[2] (some grasses). In many Lauraceæ some of the anthers are extrorse and others introrse in the same flowers; while in passion-flowers, Oxalis, &c., the anthers are at first introrse, but become afterwards extrorse.

Union of the Lobes.—The lobes of the anther may be united in three ways: 1. by simple union of their sides; 2. by means of the summit of the filament on either side of which they are placed; 3. by the intervention of the connective, which, in such cases, is found in greater or less quantity and of varied form.

Dehiscence.—As the anthers develop and contain the pollen, they must in due season dehisce, or open, to allow of the escape of this substance, the production of which is the sole essential use of the stamen. This opening or dehiscence is accomplished in different plants in different ways. Four leading methods can be recognised. 1. Where the anther opens by its whole length along the line of the furrow. This is the most common mode of dehiscence, and is seen in the lily, tulip, &c. 2. The *apicular* method, in which the anther opens by a pore at the apex of each lobe, as seen in heaths, *Vaccinium*, *Pyrola*, *Dianella cærulea* (fig. 211), all the genus *Solanum* (among others the potato), &c. In some cases there is only one pore common to two thecæ; and in the order Melastomaceæ the pores open into a little tube, through which the pollen has to pass before being discharged. 3. In the laurels, barberry, &c., the anther opens by one or two little valves,

---

[1] *Antheræ anticæ* (Robert Brown).

[2] *Antheræ posticæ* (of the same botanist).

like trap-doors, on the side, more or less to the inner face. This *valvular* dehiscence is shown in fig. 206, where there are four thecæ and four valves. 4. The last and rarest mode of dehiscence is exhibited by the genus *Pyridanthera*, in which the pollen escapes by a transverse opening which allows the top of the anther to be lifted off, like an operculum or lid.[1] Something similar occurs in *Achemilla arvensis* and *Lemna*, where the anther dehisces by a transverse opening.

Fig. 208.—Stamen of *Nerium Oleander*, L. *fl* Filament; *an* Thecæ of the anther longitudinally prolonged into horn-like prolongations at the base; *a* Long terminal prolongation of the connective.

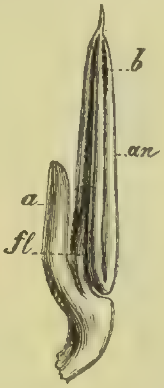


Fig. 209.—Entire stamen of *Borago officinalis*, L. (borage), viewed in profile. *fl* Filament, much shorter and more slender than its appendage *a*; *an* Anther; *b* Line of dehiscence.

Fig. 210.—Flower of *Rubia tinctorium*, L., in longitudinal section, and showing the introrse anthers. *ov* Ovules; *d* Disc.

Union of the Anthers.—1. The anthers are usually free, but it

---

[1] For some anomalous states of the anther and its dehiscence, see Robert Brown, Trans. Linn. Soc., xxiii. 214 (Collected Works); Gardner, Contributions to a Flora of Ceylon (under *Duris Zeylanicus*); Zuccarini, Ray Soc. Reports on Progress of Botany, 1845; Griffith, Trans. Linn. Soc., vol. xx. (Cryptocoryne ciliata); &c.

may also happen that all the anthers in an andrœcium may be so soldered together as to form a tube. Such stamens are styled *Syngenesious*,[1] or *Synantherous*.[2] We see this in the whole order Compositæ, or, as it is sometimes called on this account, Synanthereæ (*e. g.*, the daisy, dandelion, sunflower, chicory, hawkweed, &c.) We also see it in the case of the violets (fig. 207), and in a more marked degree in the ordinary balsam (*Balsamina hortensis*, fig. 212). 2. In a few cases not only are the anthers united together, but the filaments are also coalesced — *e. g.*, in the melon, gourd, and Lobeliaceæ. Such stamens have been called *Symphysandrous*. In *Salix monandra* there is popularly supposed to be only one stamen (hence the name); but in reality the two stamens characteristic of the willow (fig. 166) are there, but both are coalesced into one. The same explanation of the seemingly monandrous melons, gourds, and other Cucurbitaceæ, holds true. For instance, in the bryony (fig. 213) there exist a calyx and corolla, each with five divisions, but only three stamens, remarkable for their peculiar sinuous and consolidated anthers. Of these three stamens two are shaped as in fig. 210, A, while the third is represented at B. In reality, however, it is most probable that each of the two large stamens is formed of two, like that figured at B, coalesced, so that the flower has five unilocular stamens reduced by this coalescence to three.[3] Clarke and Naudin, it ought, however, to be mentioned, consider that the Cucurbitaceæ have really three stamens, of which two are complete, and provided each with a bilocular anther; while the third is only half a stamen, with a single theca. 3. Lastly, the stamens may not form a distinct verticil around the gynœcium, but may be so united together as to

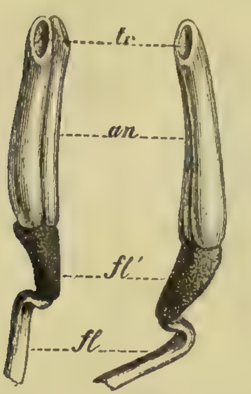


Fig. 211.—Full-grown stamen of *Dianella cærulea*, Sims, seen in two portions. *tr* The two terminal pores of the anther *an*; *fl* Filament bent, and forming a "knee" under the more thickened portion *fl'*.

Fig. 212.—Reproductive organs of the common *Balsamina hortensis*, Desp.; five stamens adherent among themselves by means of the anthers.

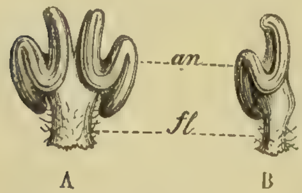


Fig. 213.—Stamens of *Bryonia dioica*, L. A, One of the large ones. B, The small one: *fl* Filament; *an* Anther.

---

[1] συν, with; γένεσις, generation.

[2] σύν, with; *anthera*, anthers.

[3] Duchartre, l. c., 537.

appear a single body, as in the birthworts (Aristolochiaceæ), all orchids, &c. Such stamens are called *Gynandrous*,[1] and the body which results from such a union is known as the *Gynostemium*,[2] or column. It may occasionally happen that the anther may become one-celled by the confluence of two thecæ into one, or *dimidiate* by the suppression of one lobe. The *Gomphrena*, or globe-amaranth of America, is a specimen of the first, while the reniform unilocular anther of the mallow affords a type of the second-mentioned method.

Colour of the Anther.—This varies from yellow, the usual colour, through all shades of red (peach) to purple (poppy, tulip), &c.; but the colours change in course of growth, more especially after their dehiscence.

Structure of the Stamen in general.—The anatomy of the filament is not the same as that of the anther. The *filament* commonly consists of a central non-ramified fibro-vascular bundle, which stretches from its base to its apex. This is covered with an envelope of cellular tissue, which often contains starch-grains. The whole is covered by a true epidermis. When the connective is present, the fibro-vascular bundles do not penetrate it. This *connective* is solely formed by cellular tissue, commonly distinct from that of the filament. When the connective is not prolonged to the termination of the two lobes, then it follows that the anther looks as if bifid, or in the form of the letter X, as is seen in grasses (fig. 214). Again, in some plants the connective spreads out horizontally, so as to form a little neck at either side of the apex of the filament, which separates the lobes of the anther con-

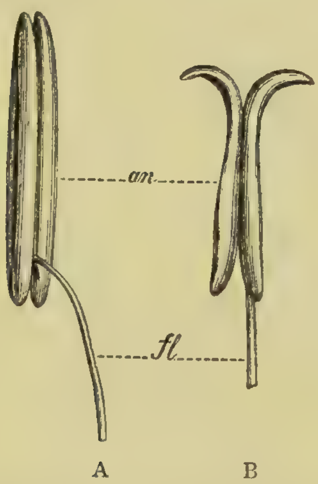


Fig. 214.—Stamen of *Lolium perenne*, L. A, Before opening; B, After opening.

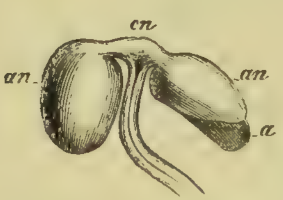


Fig. 215.—Stamen of *Mercurialis annua*, L. *an*, *an*, The two thecæ of the anther, of which one is open at *a*, borne on a long transverse connective *cn*; the vascular bundle can be seen through the transparent filament.

---

[1] γυνὴ, and ἀνηρ.

[2] γυνὴ, and στήμων.

siderably from each other. A good example of this is seen in the common mercury (*Mercurialis annua*) represented in fig. 215. Such an anther is termed *distractile.* In the sages it is even more developed—in this genus (*Salvia*) two of the lobes being deformed and sterile, and two of the four stamens being atrophied. When speaking of the appendages of the anther, we noted how in some other cases the connective projects above the apex of the anthers, either in the form of a rounded lobe (as in the so-called "Papaw" of North America, *Asimina triloba*), or of a more or less acute point (as in Magnolia, tulip-tree (*Liriodendron*), and various Zingiberaceæ, &c.) In Asclepiadaceæ it takes the form of a kind of horn.

Structure of the Anther.—The wall of the anther is formed of two distinct layers: 1. An exterior one, composed of true epidermis, called the *Exothecium*,[1] often pierced with stomata. 2. An interior one, or *Endothecium*,[2] made up of several superincumbent layers of fibrous cells (fig. 216).[3] This fibrous layer is formed out of cells which were originally closed and composed of two parts — viz. (*a*) a large vesicle; and (*b*) a spiracle, formed of branching threads in the form of a thickening on the cell-walls. Sometimes these threads are rolled up in a helicoid or snail-shell-like manner; at other times they are anastomosed into a veritable network. In the progress of growth the membrane between the threads becomes absorbed and obliterated, and nothing remains but the network formed of these threads. The whole surrounds a cavity filled with pollen, the structure and development of which we will consider presently. This fibrous layer gradually decreases in thickness as it approaches the line along which the anther dehisces, until at this point it is entirely obliterated. The use of this fibrous lining of the anther is not very clearly made

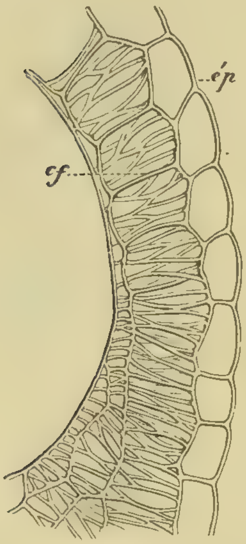


Fig. 216. — Transverse section of the walls of the anther of *Lilium superbum*. *ép* Exothecium; *cf* Layer of fibrous cells (mag. 100 times).

---

[1] ἔξω, without; θήκη, lobe.

[2] ἔνδον, within.

[3] These names were originally applied by Purkinje (De Cellulis Antherarum Fibrosis, 1830), and are sufficiently descriptive of the two layers which are found in the walls of the adult anther. In the young state of the organ there is, however, found a third delicate—almost gelatinous—layer lining the cavity, which disappears in progress of growth. Schleiden therefore distinguishes in the young anther, an *Exothecium*, a *Mesothecium* (μέσος, middle)—which is the second coat in the adult state—and this transitory layer, or *Endothecium*, as he calls it.

out. The elastic and hygrometric character of these threads enables them to contract and lengthen, according to the state of the weather, and so assist in the discharge of the pollen. And no doubt in many cases this is the function they subserve. In some instances, indeed, such as lilies and grasses, the outer layer of this fibrous coat contracts more than the inner, and so not only opens the anther—along the line of suture—but absolutely turns it inside out. In those anthers which have a valvular dehiscence, it assists by the same means in raising the valves. On the other hand, numerous plants could be named in the anthers of which this fibrous layer does not exist at certain places, and is so situated as to render it doubtful whether it does not, in many cases at least, take a very passive part in the discharge of the pollen.[1]

Attachment of the Filament to the Anther.—There are three principal ways in which the filament is attached to or joins the anther—viz.: 1. When it is *innate* or basifixed; here the filament is attached at the very extremity of the base of the anther, as in the mallow, &c. (fig. 202). 2. When it is *adnate*, mesofixed or united in the median groove along the whole length of the anther, as in the buttercup, &c. 3. When it is *versatile*, or united by its apex to a point about the middle of the median groove, so that the anther oscillates as if on a pivot by the slightest motion or the smallest breath of wind. This is exceedingly well seen in grasses, *Amaryllis belladona*, the evening primrose, &c. (fig. 214). Finally, Richard distinguishes a fourth method (as seen in *Westringia*, the Pyrolas, &c.), in which the apex of the filament is attached to the apex of the anther. These *apicifixed* anthers are, however, only a variety of the versatile mode of attachment.

Insertion of the Stamens.—The mode of insertion of the stamens affords most important characters for the co-ordination of natural groups, and may be either *relative* or *absolute*—*i. e.*, in the first case we concern ourselves with the manner in which the stamens are situated in regard to the pistil, and speak of them being inserted *on*, *around*, or *below* the ovary. In the second case the stamens are *inserted on* the calyx, the corolla, the receptacle, &c. In reference to the relative insertion of the stamens, we distinguish four different modes, expressed by special technical expressions. These are: 1. *Hypogynous*[2] if they are inserted below the ovary—*i.e.*, on the receptacle—and not united to any other organ. *Ex.*, Buttercup, flax, poppy, Cruciferæ, &c. 2. *Perigynous*[3] when they are partially adnate to any part of the

---

[1] For a full account of this see Chatin, Comptes rendus, lxii. (1866) 172-176.

[2] ὑπό, under; and γυνή, wife (by which *female* is understood).

[3] περί, around.

calyx, so as to appear to grow on it, but are quite free from the ovary. *Ex.*, The cherry, hawthorn, and the order Rosaceæ generally, purslane, &c. (figs. 217, 220). 3. *Epigynous*[1] when they adhere more or less to the ovary, so that their free tops seem to be seated upon it, and the ovary, of course, appears beneath the apparent insertion of the stamens, or is *inferior*. *Ex.*, The ivy, cranberry, the carrot, and the Umbelliferæ (hemlock order), &c. (figs. 218, 219).

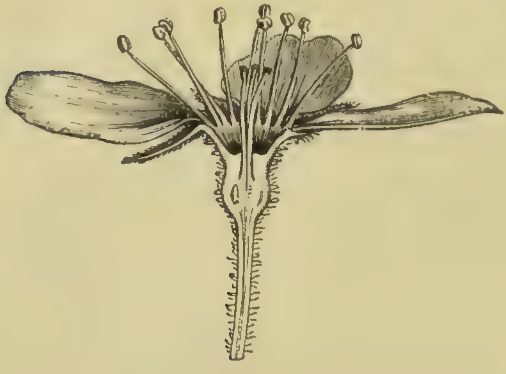


Fig. 217.—Longitudinal section of the flowering of the common Pear (*Pyrus communis*), with numerous perigynous stamens, though the ovary is inferior.

Fig. 218. — Longitudinal section of the flower of the Fennel (*Fœniculum officinale*, All.), with epigynous stamens and inferior ovary.

When the limbs of the petals do not cohere *after they separate from the ovary*, they are usually looked upon by descriptive botanists as distinct petals. 4. *Epipetalous* when the stamens partially adhere to the inner side of the corolla, so as to be "inserted" upon it. *Ex.*, The dead-nettle, *Campanula*, and the whole division of dicotyledonous flowering-plants styled *Corolliforæ* (fig. 193).

Though in general these modes of insertion prevail through whole natural groups, yet we occasionally find exceptions. Thus the pear (fig. 217), though belonging to a group in which the insertion of the stamen is essentially perigynous, has the ovary inferior; and not unfrequently we find transitions between the different forms of insertion. Nevertheless, when, as in the case of the pear, all the other characters of the flower agree with the great natural group in which the stamens are perigynous, it is placed in that division.[2] The same terms are used to express the mode of insertion of the corolla as the stamens. Thus, in all gamopetalous corollas the stamens are inserted on, or rather it would be more correct to say coalesced inferiorly with, the internal face of the corolla. Accordingly, it is the insertion of such a

---

[1] ἐπί, upon.

[2] Brongniart unites Jussieu's perigynous and epigynous stamens under one head, so that he only recognises the two categories of hypogynous and perigynous stamens.

staminiferous corolla, not the stamens themselves, relatively to the ovary, which is taken into account. Thus, we speak of the staminiferous gamopetalous corolla of the Labiatæ, &c., being *hypogynous*, that of the Ericaceæ (heaths) being *perigynous*, and, finally, that of the Rubiaceæ, Compositæ, &c., being *epigynous*. In reality, however, these terms, though convenient, are inaccurate if they are taken literally. All stamens originate in the space between the base of the petals and the base of the ovary; and when they seem to be inserted elsewhere they are only adherent to, or coalesced with, the parts on which they seem inserted.

Fig. 219.—Longitudinal section of the flower of *Fuchsia splendens*, Zucc. *ov* Inferior ovary; *s* Calyx with long tube, at the orifice of which the petals (*p*) and the other stamens are inserted, both being epigynous.

Fig. 220. — Longitudinal section of the flower of *Cerasus Caproniana*, DC., with numerous perigynous stamens.

When the stamen is longer than the perianth, the apex of it overtops the floral envelopes, and accordingly it is styled *exserted*, as in the sensitive plant (*Mimosa pudica*, fig. 221); when the contrary is the case, as in the heath, it is called *included;* if the stamens all bend to the side, they are said to be *declinate*. If there are two verticils to the andrœcium, then, in general, the most exterior one is superimposed on the corolla; and if there is a difference in the size of the stamens in such an andrœcium, then it is the interior ones which are the smallest (figs. 225, 226, 227).

Relation of the number of Stamens to the number of Petals.—We are thus led to remark that the number of the stamens does not always agree with the number of the petals. In some cases there are a great number of stamens. For instance, in the mallows (fig. 227) there are five whorls or verticils, each verticil being composed of ten stamens; while the corolla is composed of only a single verticil of five petals. Again, when there are two whorls of stamens, the number in each whorl is not always

Fig. 221. — Stamens of the sensitive plant (*Mimosa pudica*).

Fig. 222.—Diagram of the flower of *Anemone nemorosa* (one of the Ranunculaceæ).

the same. We have an example of this in the case of the flowering rush (*Butomus umbellatus*). The exterior verticil is composed of six stamens arranged in two; while the interior verticil is composed of only three stamens. In gamopetalous flowers there is usually only one whorl of stamens. The heaths (*Erica*) are exceptions, however, to this rule, there being two verticils in this genus.

Fig. 223.—Diagram of the flower of the Whin (*Ulex*), one of the Leguminosæ.

Fig. 224.—Diagram of the flower of the Wallflower (*Cheirianthus Cheiri*), one of the Cruciferæ.

Staminodia.[1]—On examining the figure of the stamen from the cinnamon plant (fig. 206), two organs will be seen near the base of it. These are imperfect, and accordingly sterile stamens. Again, in the flower-bud of *Lopezia racemosa* there are two opposite stamens. One of these remains normal, while the other has

---

[1] *Parastemina* of Link, while Dunal styles them *lepala*.

degenerated into a spoon-shaped petal, notched at one end, and terminating at the other in an elastic claw. In this case the claw is the original filament of the stamen, the spoon-shaped termination the anther; while the notch indicates its division into two lobes (Duchartre). It is remarkable that in the young state (fig. 228) this false petal is interposed between two pairs of true petals, covered by one (*c c*), and in its turn covered by others (*c' c'*). Such abortive transformed stamens are called *staminodia*, and in some cases all the stamens are so transformed into petal-like organs, as in "double flowers." These are occasionally found wild, and are more commonly produced by the unnatural conditions under which the plant is placed when cultivated. When any organ is transformed into stamens, the teratological change is termed *staminody*, while the change of stamens or other organs into petals is *petalody*. Botanists look upon "every appendage or process or

Fig. 225.—Diagram of the flower of a Peach (*Amygdalus Persica*), one of the Rosaceæ (stamens indefinite).

Fig. 226.—Diagram of the flower of an Almond (*Amygdalus communis*) (Rosaceæ), in which the stamens are indefinite in number.

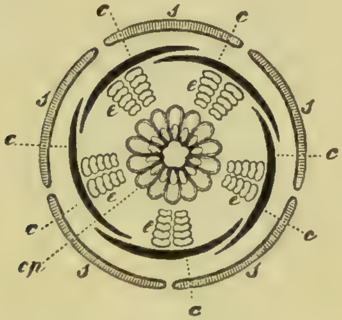


Fig. 227.—Diagram of the flower of a Mallow (*Malva*). *s* Calyx in valvular prefloration; *c* Corolla in twisted prefloration; *e* Andrœcium; *cp* Gynœcium.

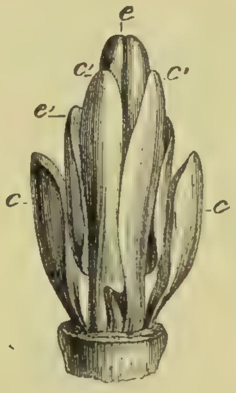


Fig. 228.—Bud of *Lopezia racemosa*, Cav., deprived of the calyx in order to show the staminodia (mag. 6 times).

organ which forms part of the same series of organs as the true stamens, or which originates between them and the pistil," as belonging to the andrœcium; but it is not always an easy matter to determine, in particular cases, whether these "staminodial" organs belong to the stamens or to the petals.

Morphology of the Stamen.—The stamens, like the petals and sepals, are only modified leaves, though further removed from the leaf type than either of the floral envelopes. Hence it is more difficult to trace the different parts of a leaf in a stamen; and accordingly there is considerable difference of opinion as to the exact morphology of the different parts, and how far they are homologous with certain parts of the typical leaf. On this subject, however, there are two main views held. Of the one Schleiden is the exponent, while Mohl's name is attached as the originator of the second. According to Schleiden (1), the connective is the median nerve or midrib; (2) the lobes are the two sides of a leaf, each rolled round towards the midrib; (3) the under surface of the leaf is therefore the outside, and the upper surface the interior lining of each theca, while the epidermis and nerves are not developed on the inside; (4) the pollen is formed from the parenchyma of the leaf; (5) when the filament is present it represents the petiole of a petiolate leaf, while, if it is wanting, then the primitive leaf was sessile. Mohl, on the other hand, taught that each part of the leaf doubles in thickness, so as to form the two thecæ of the anther, and that the pollen is formed from the parenchyma of the leaf.[1] According to his view—which is not generally adopted—the edge of the leaf constitutes the suture which runs along the theca, and by which it opens to allow the pollen to escape.[2] The theories of Mirbel, Agardh, Endlicher, Bischoff, or Wolff, we need not touch on. We thus see that leaves, bracts, sepals, petals, and stamens are only modifications of one and the same organ—viz., *the leaf;* in a word, they are *appendicular organs.*

POLLEN.

When the anther dehisces in any of the ways mentioned, a yellowish dust-like substance falls out. This is the *pollen.* On

---

[1] Though in most cases the anther is formed by the blade of the leaf, yet as we often find, as a teratological appearance, petal-like filaments bearing pollen-sacs on their sides, it is clear that we must not attribute the formation of pollen to the blade of the leaf only, but must admit that it may be formed in the filament as well (Masters, Veg. Teratology, 292).

[2] On this question see Oliver, Trans. Linn. Soc., xxiii. (1862) 423; and Masters, lib. cit., 292.

submitting this powder to microscopic examination, we find that it is composed of grains definite in shape, but different in form in different species and orders of plants. Most commonly these *pollen-grains* are single cells, globular or oval in form, yellow, and filled with a granular liquid, which is known as the *fovilla.*

Shape.—In figure the pollen-grains differ much. In general they are roundish (fig. 139), but in chicory are many-sided or polyhedral—each of the numerous faces being circumscribed by salient eminences (fig. 230). In *Basella rubra* they are square; in *Tradescantia*, &c., they are cylindrical; in musk (*Mimulus moschatus*), spirally grooved or ribbed; in mallows, *Ipomœa hederacea*, &c., covered with little eminences, so that each grain looks like a miniature sea-urchin (figs. 139, 229, 232),—and so on.

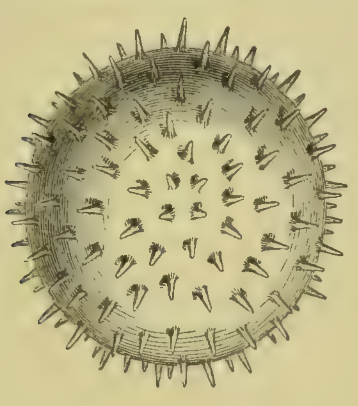


Fig. 229. — An "echinated" or "spine-covered" pollen-grain of a species of Tree Mallow (*Lavatera trimestris*, L.), mag. 200 times.

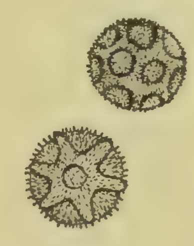


Fig. 230.—Pollen-grain of Chicory (*Cichorium Intybus*) seen on two different sides (magnified 200 times).

Fig. 231. — Pollen of the Tiger Lily (*Lilium tigrinum.* Gawl.), with a "slit." A, Viewed in front; B, Viewed at one extremity (mag. 200 times).

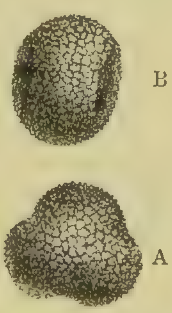


Fig. 232.—A pollen-grain of *Pelargonium zonale*, W., viewed in two different aspects to show its form. A, Side view; B, Its extremity (mag. 200 times).

Sometimes these granulations or markings on the surface of the pollen-grains are regular in their arrangement. In *Ipomœa purpurea* they form somewhat regular compartments; in *Cobœa scandens* they are in large hexagonal spaces, not regular in shape, but surrounded each by a salient crenulated lamella. These markings are formed by the external coat of the pollen-grain (which we shall have occasion to describe presently), but have nothing of the nature of a true cellular tissue in their character, as the late Hugo v. Mohl imagined. Most frequently these pollen-grains, which are marked by prominences, are also possessed of an oleaginous material, which renders the pollen glutinous; but that all pollen-grains are divisible into two categories, as Guillemin[1] thought—spiny and glutinous, and the smooth and non-glutinous—is erroneous. All pollen, when first emitted from the anther, has a slight mucosity, and the smooth as well as the hispid grains have the power of secreting a viscid substance. It has even been attempted by Guillemin, Brongniart, and Mohl,[2] and still more lately by Bailey,[3] to distinguish great natural orders, and even species, by means of the form of the pollen-grains. The Compositæ, for instance, have three or more well-marked types, such as that which we have figured from the chicory (fig. 230), the minute, oval, spiny pollen of the Asters, Calendulas, Cacalias, &c.; and a third form wholly destitute of spines, as in the great knapweed (*Centaurea scabiosa*). The different species of the same genus are also distinguished by different-shaped pollen-grains. For instance, that of *Anemone sulphurea* is roundish, but that of *A. montana* is elliptic, &c. The pollen of the orders Geraniaceæ and Campanulaceæ is for the most part globular. This is not, however, regular; for while some of the grains are quite smooth, others are covered with spines. On the whole, however, the characters derived from the pollen are, unless in a few very exceptional instances, too variable to be depended on for specific distinctions.

Size.—The dimensions of the pollen-grains vary much. All of them are so small that if their form and other characters are to be made out with anything approaching to accuracy, recourse must be had to the microscope. Some, like those of *Nyctago longiflora*, are comparatively large; while others, like those of *Myosotis* and *Lithospermum*, are very small. Between these extremes are to be found pollen-grains of every size. According to Schacht, the grains of the first-named species are $\frac{3}{20}$ of a millimetre, while those of *Convolvulus Batatas* are $\frac{1}{10}$ of a millimetre in diameter. On the other hand, those of *Ficus elastica*, according

---

[1] Mém. de la Soc. d'Hist. Nat. de Paris, ii., 1825.

[2] Uber den Bau und die Formen der Pollen Körner (Verm. Schrift.); and Ann. des Sc. Nat., 1835 (iii.), 148-180, 220-236, and 304-346.

[3] Nature, Jan. 13, 1870, 297.—(Report, Manchester Lit. and Phil. Soc.)

to the same eminent observer, are not over $\frac{3}{400}$ of a millimetre. The species of the same genus will also vary much in the size of the pollen-grains. For instance, Gulliver has shown that those of *Ranunculus arvensis* are nearly twice the size of those of *R. hirsutus*. Again, the pollen-grains of *Silene acaulis* are, according to the measurement of Mr Charles Bailey, already quoted, but half the size of those of *S. alpina*—the latter having some beautiful markings in addition. The pollen-grains of this genus differ from the usual caryophyllaceous type in not having the pits or depressions common to the order, so that the grains become spherical rather than polyhedral.

Structure.—Each pollen-grain is, in the vast preponderance of plants, made up of two superimposed coats, or of two vesicles, one within the other, and closely applied to each, the whole surrounding the *fovilla* in the interior. The action of reagents proves the chemical composition of these coats to be cellulose. 1. The exterior coat or *exine*,[1] or *extine*,[2] is comparatively thick, and resistant with little elasticity, so that it breaks easily when distended, and is often granular or fleshy in appearance. It is formed or secreted from the inner one, and all the markings belong to it. It can, though with difficulty, be separated from the pollen-grain, if this is macerated in slightly acidulated syrup. Mohl's idea that it is analogous to the cuticle is not borne out by recent observations on its development. 2. The *intine* or inner coat is the proper cell-membrane. It is very thin, but of considerable strength for its thickness, and is without a trace of organisation. We have already referred to Mohl's idea that in some cases—among others *Nyctago hortensis*, *Hemerocallis fulva*, *Statice latifolia*, &c.—the exine partakes of the nature of a cellular tissue, an idea not entertained by the great body of Phytotomists, who are almost at one in the belief that neither coat of the pollen-grains shows the slightest appreciable structure. The same botanist announced many years ago that in some genera of Coniferæ (Yew, Juniper, Cypress, and Arbor-vitæ), Gourd (*Cucurbita Pepo*), *Tigridia Pavonia*, there are three coats, the two interior being very thin and diaphanous. Meyer and Schacht have shown that in some pollens, at least (Œnothera, Clarkia, &c.), the outer coat of the grain may be divided into two layers (fig. 233 B, *a* and *a'*), very distinct over the whole of the grain, but coalesced at each of the three eminences which characterise the grain; though I am not aware that any other observer has confirmed Fritzche's assertion that in the

---

[1] These names were originally given to the coats of the pollen-grain by Julius Fritzche (Mém. de l'Acad. impér. des Sciences de St Petersbourg, 1837); but in the next year (1838), Richard, in ignorance of the prior nomenclature of Fritzche, named them anew the *Exhymenium* and *Endhymenium*.

[2] This Fritzche calls the *exintine*.

pollen of certain Onograceæ there are even four coats.[1] On the other hand, in *Zostera*, and some other aquatic plants (*Zannichellia, Naias, Caulinia, Ruppia*), the pollen of which is peculiarly formed (p. 346), there is no outer coat.

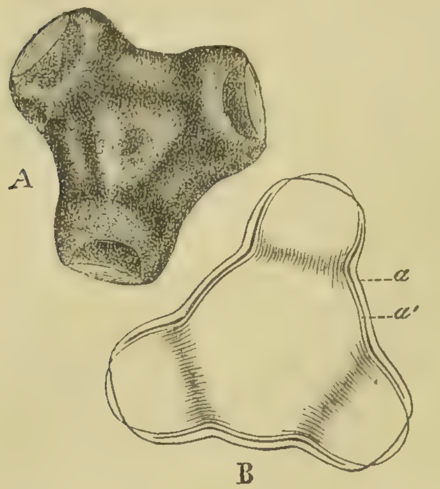


Fig. 233.—Pollen of *Clarkia elegans*, Dougl. A, Seen a dry object. B, Seen in water; *a a'* The two layers of extine (mag. 200 times).

Fovilla.—The interior of the pollen-grain is filled with a viscid liquid, rich in protoplasm, which, under the microscope, often appears slightly turbid, though in many cases transparent and often uncoloured. Under still higher power—say 300 diameters—it is found that this fluid, to which Martyn gave the name of *fovilla*, is filled with minute particles, unequally-sized and variable in form, the largest of which are from 4000-5000 of an inch in length, and the smallest only one-fourth or one-sixth of that size.

Movements in the Fovilla.—Count Gleichen, many years ago, described curious movements of these particles in the fovilla, which Brongniart[2] and others considered spontaneous, comparing the fovilline particles to the spermatozoa of the animal generative fluid. It is now, however, universally believed that these movements are in no respect of this nature, but come under the same category as those observed in any fluid where exceedingly minute bodies—even inorganic—are contained, and which, out of compliment to the discoverer, the late Robert Brown, have been called the "Brownonian movements." In the cylindrical thread-like pollen-grains of *Zostera*, &c., already described, there is a circulation very similar to what we observe in the articulations of *Chara* and the cells of various other plants (p. 20). It may be remarked, however, that unless these marine plants just named form an exception, all movement of the fovilla in the pollen-grain has ceased by the time the pollen leaves the anther. When the pollen-grain falls on the stigma, the inner coat, as we shall see presently, develops outward in the form of a tube. Into this tube Amici,[3] and others since then, have observed the fovilla "flowing downwards in a broad stream and back on the opposite side."[4] Sac-

---

[1] The fourth he called *intexine*.

[2] Ann. des Sc. Nat., xii. 40, and xv. 381.

[3] Ibid., ii. 68.

[4] Mohl, Veg. Cell, 128.

cardo[1] announces that he has detected in the fovilla small bodies exhibiting Brownonian movements, and making up its bulk. These he calls *somatia.* Their form is invariable in the same species of plant, and in plants of the same genus the form appears to be nearly identical. In the hollyhock they are disciform, in *Portulaca grandiflora* fusiform, &c. To see them, a magnifying power of from 800 to 1000 diameters is required. Treated with iodine, they take a blue colour, but only on the portion outside, the interior remaining clear.

Chemical Composition of the Fovilla.—If further proof were necessary of the vegetable nature of the fovilline particles, it is supplied by the discovery of Fritzche that granules of starch and sometimes of inuline, which are coloured blue and sometimes yellow by iodine, accompany the minute drops of essential oil which swim in the fluid. It is these granules which perform the molecular Brownonian movements about which there has been so much controversy. In addition, the fovilla also contains a certain proportion of sugar, which, under the action of sulphuric acid, turns to a rose colour, and various other azotised materials. Geraud found in the pollen of the snapdragon (*Antirrhinum majus*) potassa, and raphides of phosphate of lime among that of the Virginian spiderwort (*Tradescantia virginica*). Fourcroy and Vauquelin found malic acid in the pollen of the date-tree, and Macaire-Prinseps malate of potash and other salts in that of the cedar.[2] In addition to sugar, gum, albumen, cerin, resin, &c., Herapath[3] found as much as 46 per cent of a peculiar inflammable azotised principle, insoluble in nearly every liquid, which Girardin[4] called *Pollenine*, in the pollen of *Cereus speciosissimus*, and nearly as much in two species of lily. Lastly, the outside of the pollen-grains of several genera—*Phormium*, *Scorzonera*, *Nyctago*—are surrounded with a thick oil, which gives a colour to the pollen. This oil may be a secretion of the mother cells (p. 344) of the anther, and is certainly contained in the walls of the anther. In the genera *Gossypium*, *Molopa*, and all the Onograceæ, the oil is replaced by a glutinous substance (p. 338).

Pores and Slits of the Pollen-Grain.—If the pollen-grain is brought into contact with water, owing to all the conditions for its exercise being present, endosmose immediately commences with great rapidity—the result being that the coats are ruptured, and the pollen-grain prevented from fulfilling the purpose which it is intended to subserve in the fecundation of the ovule, and the consequent production of the seed. Hence a

---

[1] Nuovo Giornale Bot. Ital. (*teste* Pop. Sc. Rev., 1873, 307).

[2] Bibliotheque Universelle, 1830, 45.

[3] Pharmaceutical Journal, Feb. 1848.

[4] Leçons de Chimie Elémentaire, 3d ed., p. 839 (*teste* Lindley).

wet season is unfavourable for the ripening of grain and other fruits. In Holland it is always noticed that after a wet season there is a poor juniper crop. If, however, it is brought into contact with some thicker liquid than water—syrup or mucilage, for instance, or some substance of a similar consistency—then the endosmotic action takes place much more slowly. The grain swells, and any inequalities on the exterior get smoothed out; the grain also changes its shape, somewhat getting rather more ellipsoidal; and if absorption continues, the outer coat will burst, and the inner will protrude through it in the form of either one or more slender delicate tubes closed at the outer end. If the pollen-grain has fallen on the surface of the stigma, which is generally moist or viscid, this action takes place; and, as we shall have occasion to describe in the course of a future chapter (ch. viii.), this *pollen-tube* with its fovilline contents, after penetrating through the stigma and style, enters the ovule or young seed, performing thereby the most essential process of fertilisation. The places where these tubular protrusions of intine take place are generally at the poles of the pollen-grain. But in many cases the tubes protrude through special portions of the pollen-grain, where the coats are thinner than over the rest of it. These spots are known as pores (or *oscula*), pits, or depressions, and, when more elongated, *slits* or folds—neither name, however, requiring to be received in its ordinary acceptation, as in no case are both the coats entirely interrupted at the pores or slits so called. In the pollen-grain of some plants (laurels, Aroïdeæ, and Aristolochiaceæ) neither are present; while in other plants the numbers and position of the pores and slits are rigidly determined. The slits are generally longitudinal, from pole to pole, in the median line of the pollen-grain (*Plumbago Zeylanica*, lily, fig. 231, &c.) In most cases only the intine is present; but in some plants the exine is also present in the form of a thin layer at the bottom of the slit, even though the rest of the pollen-grain is reticulated or corrugated; but in every case the margins of the slits are bounded by the thickened fold of the exine in the form of a ridge-like eminence. The *number* of the slits varies. In most Monocotyledons there is only one (Liliaceæ (fig. 231), iris, palms, &c.); the number three is frequent among the Dicotyledons (roses, Leguminosæ, Solanaceæ, Cruciferæ, &c.); more than three is rare, but from four to six are found on the common borage, and various other Boraginaceæ, Labiatæ, Rubiaceæ, Apocynaceæ, &c.

Pores are found on the pollen-grains of many plants. They are circular thinnings of the exine, through which the intine can be seen at the bottom, though Schacht asserts that in some cases, at least, there is not a mere thinning of the outer coat, but an absolute deficiency of it. The number of pores is also very variable. On the pollen of *Limodosum*, *Furcroya*, *Amona*, *Oreodaphne*, *Persea*, wheat and most other grasses, Cyperaceæ, &c., they have not been observed in greater numbers than one; two are found on the paper-mulberry, *Colchicum*, and *Broussonetia*, but this number is rare. Three are seen on *Œnothera biennis* and other Onograceæ, and on the pollen of the orders Proteaceæ, Urticaceæ, Dipsacaceæ; there are four on balsam, *Trigonia*, *Fumaria* (fig. 234), &c.; while on *Nyctago hortensis* there are as many as 100. It is even said that on the hollyhock (*Althæa rosea*) as many as 200 have been counted. The following table, compiled from Mohl, Duchartre, and others, presents these curious facts in regard to the absence, presence, and number of the pores and slits of the pollen-grains in a synoptical form:—

Fig. 234.—Pollen-grain of Fumitory (*Fumaria officinalis*, L.), showing four of the great pores on it (mag. 200 times).

I. **Pollen without either Pores or Slits.**—Most Araceæ, Musa, Strelitzia Reginæ, Canna; Laurus, most Euphorbiaceæ, Ranunculus trilobus, &c.

II. **Pollen with Slits, but no Pores.**—(α) *One* pore: most Monocotyledons; and, among Dicotyledons, Salisburia, Magnolia, and Nymphæa, most markedly. (β) *Two* slits: rare, Dioscoreaceæ, Tigridia, Cypripedium, Calycanthus, &c. (γ) *Three* slits: most Dicotyledons, oak, Cereus, mistletoe, &c. (δ) *Four* slits: rare, Sideritis scordioides, Houstonia coccinea. (ε) *Six* slits: various Labiatæ and Passifloræ. (ζ) Slits *more numerous than six:* many Rubiaceæ; Penæa, Sesamum.

III. **Pollen with Pores, but no Slits.**—(α) *One* pore: Grasses, Cyperaceæ, Anona, Cecropia. (β) *Two* pores: rare, Colchicum, Broussonetia. (γ) *Three* pores: Onograceæ, Proteaceæ, Urticaceæ, Dipsacaceæ. (δ) *Four* pores: Balsam, Phyteuma, Trigonia. (ε) Pores *more numerous than four:* (1) *Situated on the equatorial line* of the pollen-grain—alder, willow, ash, Collomia; (2) *Scattered*—Nyctaginaceæ, Convolvulaceæ, Caryophyllaceæ, Cucurbitaceæ, Malvaceæ, Cobæa.

IV. **Pollen with both Pores and Slits.**—(α) *Three* pores and *three* slits: most Dicotyledons, and notably the Compositæ. (β) *Many* pores and slits: most Boraginaceæ and Polygalaceæ. (γ) *Six to nine* slits, and *only three* pores: (1) *Six slits and three pores*—Lythraceæ, Melastomaceæ, Combretaceæ; (2) *Nine slits and three pores*—Ammania sanguinea.

Development of the Anther and Pollen.—In the earliest period of its development—supposing it is examined in the bud—the anther is a simple sessile tubercle, composed of homogeneous cellular tissue. The apex is somewhat elongated, and is medianly divided by a delicate furrow which makes its appearance in course of time; then the filament begins to make its appearance, and a second furrow divides each lobe into four, so that in the earlier stages of the anther there are four thecæ instead of two, as in most cases in the adult condition where the embryo condition is exceptional. These external appearances point to a corresponding development going on within the anther. Making a transverse section of it, we find that in the midst of the once homogeneous cellular tissue a change has taken place. In each of the divisions corresponding to what are afterwards the two lobes of the anther, two cavities appear, corresponding to the four lobes which the longitudinal furrows on the outside of the young anther point to. At first very minute, and almost linear, they get filled by thick mucilaginous fluid, which insensibly organises itself into a cellular tissue with thickened walls, which with the epidermis constitutes the whole mass of the anther. The most exterior of the cells are very small, and become, in the manner we have already described, the *fibrous layer* (p. 330, fig. 235, *b b*). The more interior ones are large, and full of colourless gelatinous protoplasm, and constitute the *mother cells* of the pollen (fig. 235, *a*). These mother cells after a time become divided, either by the formation of transverse partitions from the walls (Mirbel, Unger, Mohl), or by free cell-multiplication (Decaisne, Nägli, Hofmeister, Wimmel, Duchartre), into four triangular cells, which afterwards become the pollen-grains (fig. 236). At first the intine is the only coat which surrounds the grains; but afterwards the exine appears, either by secretion from the intine, or by deposition, according to other observers—a doctrine warmly espoused and defended by Schacht. Subsequently the line of division between the thecæ gets, in the majority of instances, so far absorbed as to reduce

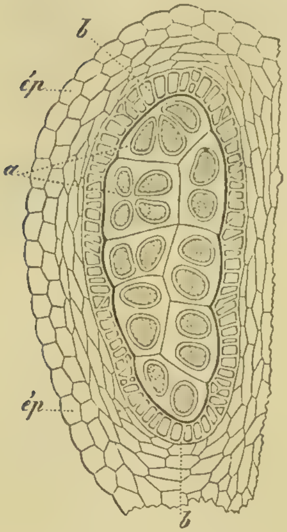


Fig. 235.—Transverse section (after Mirbel) of a theca of a Cucumber (*Cucurbita*). *ép* Exothecium; *b b* Endothecium—between the two is the middle coat or mesothecium; *a* Pollen-cells, in which are seen two, three, or in one four, grains of pollen, according as the line of section has exposed them (mag. about 250 times).

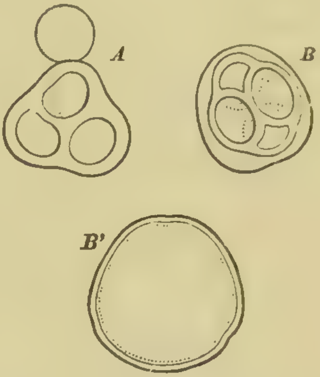


Fig. 236.—Pollen-cells of *Lathræa Clandestina*, L. A, Utricle, in which a grain of pollen is escaping; B, Utricle about to open; B', Grain full-grown.

the number to four, though in some cases a greater number remains throughout the adult state of the anther by the non-absorption of the intervening cellular tissue (p. 325).[1] Lastly, it may be mentioned that the transitory delicate lining of the thecæ, which we mentioned in a former paragraph when speaking of the structure of the anther, may be intended for the nutrition of either the mother cells, or in some way minister to the development of the pollen,[2] or to the peculiar organisation of the still more external layer. On figs. 235, 236, some of the facts given in the foregoing description are more fully explained.

Compound Pollen-Grains.—In the Coniferæ (figs. 237, 239), and various species of Onograceæ, the pollen-grains are not single cells, but are composed of three or four blended together by viscid and elastic material, so that in *Ænothera biennis* (evening primrose) *Clarkia*, (fig. 233), Epicridaceæ, &c., each grain is triangular in shape.[3] In heaths (Ericaceæ), *Leschenaultia*, &c., they are com-

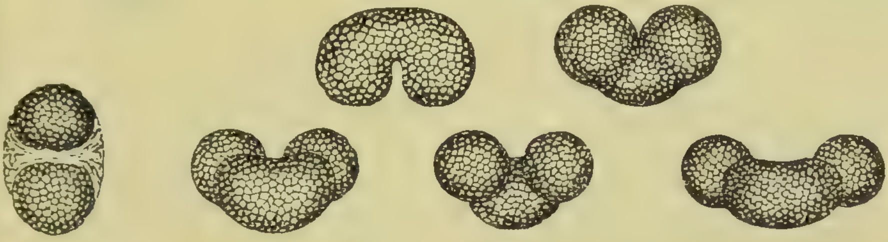


Fig. 237.—Composite pollen of the Cedar.

---

[1] The question of the development of the pollen has been the subject of numerous elaborate researches, the difficulty of the subject affording an excuse for the very contradictory statements made by different observers. We have only given an outline of the main results arrived at, touching as little as possible on controverted points; but for further information the student is referred, among others, to the following memoirs: Wimmel, Botan. Zeit., 1850, 225-235, 241-248, 265-270, 280-294, 313-320; Mirbel, Mém. de l'Acad. des Sciences, xiii., 1836; Mohl, Vegetable Cell (Engl. trans.), 57, 127, Vermischte Schriften, 42, &c.; Decaisne, Mém. de l'Acad. Royale de Brux., xiii. (1840); Nägli, Zur Entwickelungsgeschichte der Pollen, 1842; Hofmeister, Bot. Zeit., 1848, 425, 434, 649-658, 670-674, and Abhand. d. k. Sächs Ges., vii.; Henfrey, Ann. of Nat. Hist., xviii. 364; Reichenbach, De Pollinis Orchidearum genesi (1852); Rosanoff, Jahr. f. Wiss. Bot., vi. 441 (Pollen of *Mimosa*); Notes in Sach's Lehrbuch, (1873) 472; and more especially to the important treatise of Warming, Untersuchungen über Pollen bildende Phyllome u. Kaulome (Hanstein's Bot. Abhandlungen, ii. Bd. 2 h. 1873).

[2] Chatin, Comptes rendus, 1866 (lxii.), 126-130.

[3] In Coniferæ it is remarkable that it is not the intine but a secondary structure—viz., one or other of two unequally-sized cells produced in the median part of the pollen-grain—which elongates into the tube by which fecundation is effected. This curious fact was first observed by Géleznoff in 1849, but has of late been confirmed by Schacht.

posed of four grains united (fig. 238); in Mimoseæ (Leguminosæ), eight; in several Acacias, sixteen; and so on. In the Zosteras, or eel-grasses, and allied orders of flowering-plants which grow in salt water, the pollen-grains are divested of the outer coat (p. 340), and consist of long slender threads, which, as they lie side by side in the unilocular anther, look not unlike a skein of silk.

Fig. 238.—Composite pollen of *Typha* (Bulrush).

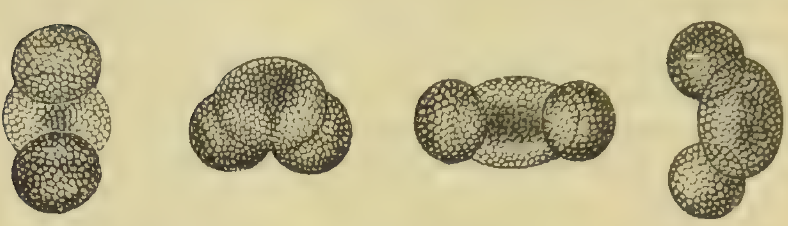


Fig. 239.—Composite pollen of the genus *Pinus*.

Solid Pollen.—As the pollen completes its growth, the walls of the mother cells are usually obliterated; but sometimes the walls of the enclosing cell remain persistent, and enclose pollen-grains of various consistence, as among the milkweeds (Asclepiadaceæ) and various families of orchids. In contradistinction to the *pulverulent pollen* found in all other orders of plants, the pollen of these orders is styled *solid*, or the combined grains are known collectively as *pollinia*, or "pollen-masses." The pollen-grains are united together either by a viscid substance, or more rarely by threads. In the evening primrose, the threads mixed with the pollen are only vestiges of obliterated mother cells. In most orchids the grains composing each pollinium are united in fours by an elastic network called the *massa sectilis*, while in *Epacris* and *Neottia* these are simply coalesced by mutual pressure in the thecæ. In this latter case the pollen is therefore still styled *pulverulent;* while in the *Malaxidæ*, another tribe of orchids, the grains are so intimately united as to make a solid mass. In *Cephalanthera* and *Limodosium* the grains of pollen remain distinct as in other plants. In some orchids (*Orchis maculata*, for example) each of these pollinia is pear-shaped, narrowed to a thin stem-like part called the *caudicle*,[1] and terminated by a glandular disc or *retinaculum*,[2] by which it attaches itself to the *rostellum*, or beak-like prolongation from the anther. In the Asclepiadaceæ there are always two of these pollinia united by their retinacula.

---

[1] *Cauda*, a tail.

[2] *Retinaculum*, rein or band.

and depending on the theca in the form of the sides of the letter V inverted. In this order a kind of cellular membrane permeates the pollen-mass, forming a great number of cells, in each of which is found a grain of pollen alike in structure to those of orchids.

The pollinia in each theca remains always separate in all true orchids (*Orchis*, *Ophrys*, and *Gymnadenia*), but they are united by their caudicle in the genera *Anacamptis*, *Himantoglossum*, *Goodyera*, *Corallorhiza*, &c. This caudicle is composed of numerous cells, which, in place of being transformed into pollen-grains, secrete a viscid substance which enables the two pollen-masses to unite. (Chap. IX.)

Lastly, the shape of the pollen-masses is generally the same as the thecæ of the anther, which have acted as moulds to them, and there may be two, four, or even sometimes eight to one anther.

Vitality of the Pollen.—Pollen may be kept in the dry state for months, and even years, and sent from country to country to fertilise plants which produce only female flowers. For instance, the date-palm is diœcious, and accordingly, from the earliest periods it has been the custom for the Egyptians to bring branches with staminiferous flowers from the desert to fertilise the pistilliferous flowers of the cultivated trees. In 1808, when the French were in Egypt, the inhabitants were thereby prevented obtaining the branches for the male flowers; and the result was, as only female-flowered trees are cultivated, no dates were produced. The pollen will also be wafted long distances by the winds, as the "sulphur-showers" in the vicinity of fir-forests prove. In 1505 it is recorded by the poet Pontanus—and by even more credible witnesses—that a female date-palm at Brindes, which had never produced, was fertilised, and in consequence matured fruit, from the pollen wafted thirty miles from another tree of the same species at Otranto; and Henslow informs us that date-trees in St Helena have been fertilised by pollen obtained from trees on the continent of Africa. Numerous similar cases are on record.

Colour.—The colour of the pollen is generally yellowish, but it varies in this respect even in the same genus. For instance, in the genus *Lilium*, all shades, from yellowish to brown, may be found. That of *Ajuga Genevensis* is yellow, but that of *A. pyramidalis* usually white. Again, the grains of *Ornithogallum umbellatum* are large and yellow, while those of *O. nutans* are small and white. In *Actæa spicata* the pollen is also whitish; while that of certain species of *Epilobium*, and many Polemoniaceæ, is bluish, and in *Verbascum* red. It is never green.

The general *teratology* of the andrœcium will be considered with that of the rest of the floral whorls, when we shall have occasion (Chap. V.) to consider the metamorphosis and symmetry of the flower.

CHAPTER IV.

THE GYNŒCIUM, OR PISTILLINE[1] WHORL.

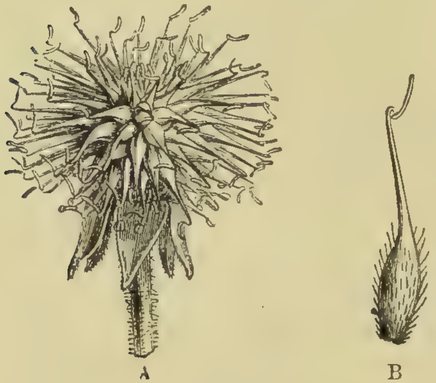


Fig. 240.—*Geum urbanum*, L. (Herb-Bennet). A, Head of the entire fruit (twice the nat. size). B, One of the little fruits or carpels isolated (4 times nat. size).

THIS constitutes the fourth, last, and in a perfect (hermaphrodite) flower the central whorl of the floral organs. The *pistil* is made up of *carpels*,[2] and may consist of a single carpel (when it is styled a *simple pistil*) or of several in union, constituting a *compound pistil*. Again, the terms *apocarpous*[3] and *syncarpous*[4] are applied to signify whether the carpels are separated one from another, as in *Caltha*, *Ranunculus*, Hellebore, &c. (fig. 240), or are in union (fig. 242). Some botanists style each separate carpel a pistil; while others, more philosophically, look upon the whole of the carpels, whether one or many, syncarpous or apocarpous, as merely constituting *a* pistil. Practically, it is immaterial which view is taken. Let us now examine a pistil consisting of a single carpel; in other words, a simple pistil. It consists of five parts—viz., 1. the *ovary*, a cavity occupying the lower part, where it joins the receptacle, and which contains the ovules or young seeds; 2. the *style*, a filiform prolongation of the summit of the ovary; 3. the *stigma*, a glandular body, terminating the style; 4. the *ovules* or young seeds; 5. the *placenta*, to which the ovules are attached. We have already noted the fact that the carpels may, like the other floral organs, be either separate or coalesced; and this union may be only by the carpels or by a part of the carpels,

---

[1] So named by Röper. It is commonly spelt in English books *gynæcium* (γυνὴ, female; οἶκος, abode).

[2] καρπός, fruit.

[3] ἀπὸ, apart; καρπός, fruit.

[4] σὺν, together; καρπός.

by the carpels and the styles, or, finally, the carpels, styles, and stigma may be all united into one body. Linnæus looked upon each apocarpous carpel as a separate pistil; and accordingly certain terms employed by this illustrious botanist are still in use to express the number of carpels entering into the composition of a pistil. Thus, a flower with a pistil composed of a single carpel,—or, as Linnæus and those who still adopt his views would say, a simple pistil—was styled *monogynous;* one with two, *digynous;* with three, *trigynous;* with four, *tetragynous;* with five, *pentagynous*, &c. When the carpels, as in a buttercup or strawberry, were numerous or indefinite, then they were styled *polygynous*. These terms only refer to *apocarpous* pistils; for in a *syncarpous* one, though to outward view there might seem to be only a simple pistil, it is in reality not so, but a compound organ formed by the intimate coalescence of two, three, four, or a greater number of carpels, as can only be seen on cutting the ovary across. We can, except in exceptional cases, speedily ascertain in a syncarpous pistil the number of carpels of which it is made up, by making a transverse section of the ovary. Here we will find a number of cavities or *loculaments*, equal in number to the number of carpels which compose the ovary. If there is only a single loculament, we conclude that there is only a single carpel entering into its composition; in a word, that the pistil is a simple one. Hence we speak of a pistil (or at least of its ovary) being *bi-*, *tri-*, or *multi- locular*, according as it presents, on transverse section, two, three, or a greater number of loculi, from two, three, or a greater number of united carpels entering into its composition. As we shall see by-and-by, there may be an exception to this rule, in so far that, by the absorption of the walls of two contiguous carpels, an ovary which in reality is made up of several carpels presents only one loculament.

It is rare that we find the separate carpels (or, to use the Linnæan nomenclature, the pistils) exactly equal in number to the sepals or petals. They are, as in the strawberry and Magnolia, where they are arranged in several rows upon the swollen receptacle, more in number, or in other cases they are fewer in number. When the pistil is composed of a single carpel, or of several coalesced into one, then such a pistil must necessarily terminate the axis of which it appears to be a direct continuation. When there are two carpels in the pistil, they always stand opposite each other (so that if they coalesce it is by their inner faces). In such a case they may be *lateral*, as respects the flower—*i.e.*, one on the right side and another on the left, in a plane at right angles to the bract and axis, as in the Cruciferæ and Gentianaceæ, &c. More commonly they are *anterior* and *posterior*—in other words, one before the axis and the other before the bract of the axillary flower. When the carpels accord in number with the sepals or petals, they are either opposed to or alternate with them; and the two positions are, in this respect, sometimes found in nearly-related genera, so that it is a puzzle to explain the cause of this difference. In *Pavonia*, for example, the five carpels which compose the pistil are opposite the petals; in *Malvaviscus* and *Hibiscus* they are alternate with them, &c.[1]

Sometimes, as in the aconite, the carpels are arranged invertically. When they are great in number the receptacle enlarges, and is called a *gynophore* (thecaphore, basigynium, or podogynium, p. 287), in which case the carpels are either placed without regard to order (Ranunculus, strawberry), or follow the spiral arrangement common in other parts of the flower (Magnolia, tulip).

Let us now consider the individual parts of a carpel or simple pistil more in detail.

Ovary.[2]—This constitutes the lower part of the carpel or carpels, when several are coalesced. In the cavity or cavities (loculaments) of the interior are contained the ovules. In *shape* the ovary is generally *ovoid* or *globular;* but it may be *elongated*, or even *linear*.

Loculaments.—The morphology of the pistil we shall have occasion to enter upon more fully after we have considered the anatomy and relations of the gynœcium; but in the mean time we may anticipate by saying that the carpels are, like the stamens, only modified leaves, though seemingly more distantly removed from the leaf type than even the stamens. Each carpel is a leaf folded upon itself until the two edges meet. Hence the *dorsal* and *ventral* sutures, seen on the back and the inner side of the carpel, are only the midrib and the line of junction of the two margins of the leaf. Now, supposing we take four or five such leaves, bend each until the two edges meet, and set the whole in a circle in contiguity, the result would be that there would be a number of cavities, each separated from its neighbour on either side by double-walled partitions formed by the contiguous sides of two leaves (fig. 241). Lastly, the number of cavities and partitions would exactly corre-

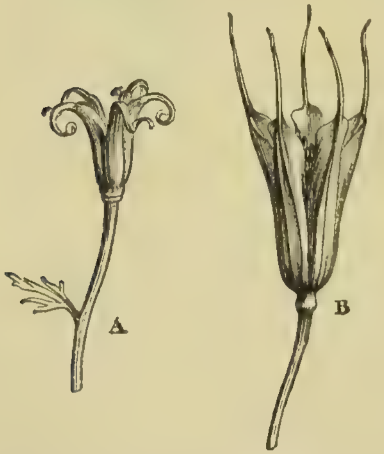


Fig. 241.—*Nigella arvensis*, (Devil-in-the-bush). A, Pistil; B, Ripe fruit opening.

---

[1] Gray, lib. cit., p. 288.

[2] *Ovarium*—the *germen* of Linnæus.

spond to the number of leaves which entered into the imaginary circle we are describing. This is exactly what we find on making a transverse section of the ovary. The cavities seen on making such a transverse section are called *loculaments*, and the partitions separating them *dissepiments* or *septa*. The number of loculaments corresponds to the number of carpellary leaves entering into its composition. If the ovary was originally composed of only one carpel—a simple pistil—then there would be only *one* loculament without any dissepiments, the sides of the leaf forming the walls of this *unilocular* ovary. But if *two*, *three*, *four*, *five*, or a *greater number* of carpels had coalesced to form the ovary, then there would be *two*, *three*, *four*, *five*, or a *greater number* of loculaments, and a corresponding number of dissepiments; while, in descriptive language, the ovary would be styled *bi-*, *tri-*, *quadri-*, *quinque-*, or *multi-* locular (figs. 242, 244, 245, &c.)

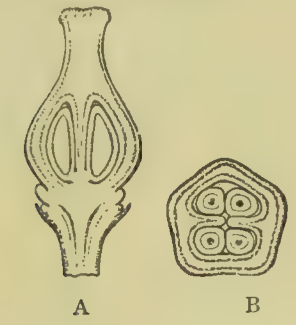


Fig. 242.—Pistil of the Vine (*Vitis vinifera*, L.) A, Longitudinal section; B, Transverse section (mag. 5 times).

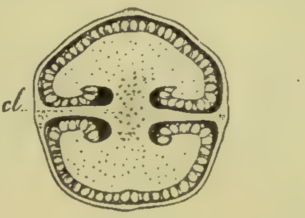


Fig. 243.—*Nicotiana Tabacum*, L. Transverse section of an ovary passing to the state of a ripe fruit. *cl* Partition, on the sides of which are borne two very thick placentas (punctated in the figure)—mag. 4 times.

Fig. 244.—*Antirrhinum majus*, L. (Snapdragon). Transverse section of the ovary passing to the state of a ripe fruit (mag. 3 times).

Fig. 245. — Transverse section of the ovary of a Pear (*Pyrus communis*), with five loculaments (mag. 6 times).

There are, however, exceptions to this rule. An ovary may consist of two or more coalesced carpels, and yet be unilocular in one or other of the following ways: 1. The natural dissepiments between the loculaments may be absorbed at an early stage of growth, as in the genera *Cistus* and *Helianthemum* (rock-roses), where the ovary is primitively trilocular. An example of this is also afforded by *Saponaria*, and other genera of Caryophyllaceæ. 2. The carpellary leaves,[1] instead of being rolled or folded on themselves, so that the edges meet so as to form the inner or ven-

---

[1] Or carpophylls.

tral suture, are united edge to edge in their flattened state, in such a manner as to form a unilocular ovary. This is the case in the violets, the poppies, &c., in which the ovary is composed of three or a greater number of carpels, but is nevertheless unilocular. In most cases, however, no real difficulty exists in ascertaining the original number of loculaments in an ovary. No carpel has more than one style surmounted by a single stigma. Accordingly, when we see an ovary surmounted by several styles, either single or coalesced, and only distinct at their summits, then we know that a number of carpels, equal to the number of styles or stigmas, or at least divisions of the stigma, had entered into its composition. The number of styles and stigmas also points out—as in grasses, Cyperaceæ, Chenopodiaceæ, &c.—an ovary originally composed of several carpels, and of which only one is developed. Lastly, whenever we find in a unilocular ovary ovules attached to several parietal placentas, then undoubtedly such an ovary is made up of several coalesced carpels.

Fig. 246.—Diagram of the flower of *Omphalodes*, one of the Boraginaceæ. The ovary is apparently quadrilocular, but in reality it is bilocular, with the loculaments each subdivided into two false uniovular loculaments.

Dissepiments.[1]—These, we have seen, are vertical partitions between the different loculaments, and, being formed by the sides of the carpels, are of course double. The dissepiments may be called (1) *true*, and (2) *false*.[2] The true dissepiments we have already described. The false ones are generally growths from the dorsal or ventral suture of one or more carpels, and never stretch sufficiently far across the ovary to form complete partitions, as may be seen in the Gentians, and more especially in the genera *Chironia*, *Chlora*, &c. In some cases (as in the *replum* of Cruciferæ) they are caused by expansions of the placenta, and in this case stretch, in the form of a membranous partition, from one side to the other of the ovary. In *Cathartocarpus Fistula*[3] Lindley has observed that they are horizontal, and are mere dilatations of the inner wall of the ovary, or of its ripened state (the pericarp of the fruit). In *Amelanchier*, *Astragalus*, and *Thespesia*, the same botanist pointed out, many years ago, that they were only expansions from one of the sutures, and can be distinguished from true dissepiments by not bearing placentæ or ovules, by being opposite the stigma, or by projecting beyond the

---

[1] *Dissepio*, I separate.

[2] Also called *spurious* and *incomplete*, in contradistinction to the *true* or *complete* dissepiments.

[3] When they are termed *phragmata* (φρᾶγμα, a separation or partition).

placentæ. Finally, as in *Diplophractum*, they may be caused by the ovary "projecting into the cavity, uniting and forming many supplementary cells." In the common thorn-apple (*Datura Stramonium*, fig. 247) the ovary is, as in the tobacco (fig. 243), bilocular; but the transverse section (fig. 248) shows four loculaments.

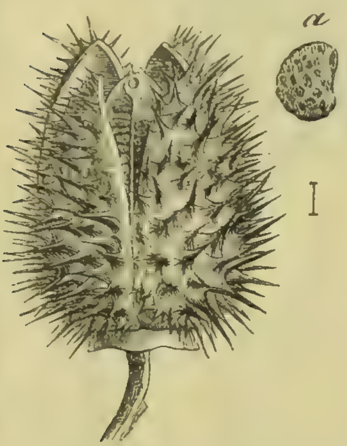


Fig. 247.—Ripe fruit of Thorn-Apple (*Datura Stramonium*), with *a*, seed.

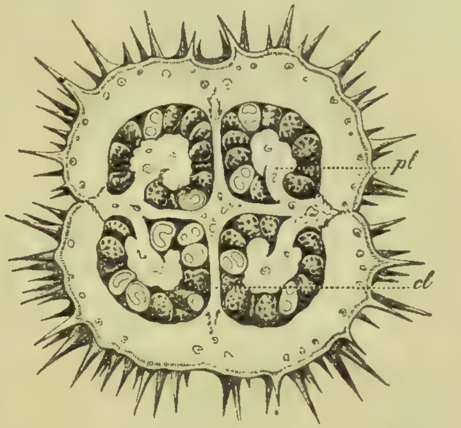


Fig. 248.—*Datura Stramonium*, L. Transverse section of the ovary passing to the state of an almost ripe fruit. *pl* The placentas; *cl* True dissepiment.

Two of these are, however, caused by false dissepiments, formed by a growth by the median line of each carpel, joining the true placenta-bearing dissepiments. The same is seen in fig. 246.

Attachment of the Ovary.—In general the ovary is inserted on the receptacle without attachment to the other floral envelopes. (1.) In this case it is called *free* or *superior*—that is, placed above the attachment of the floral envelopes. *Ex.* Poppy, tulip. (2.) In a gamosepalous calyx the ovary is often coalesced with it, so that it appears below the attachment of the calyx, and is called *attached* or *inferior*. In reality, however, all the floral organs are attached below the ovary, but from adhesion seem to grow upon it (p. 313). The terms are, however, too convenient to be disused; especially the inferior or superior ovary forms an important character to distinguish natural orders. For instance, the ovary is *inferior* in the Amaryllidaceæ, and *superior* in the Liliaceæ.

Placenta and Placentation.—At the point of junction of the two edges of carpellary leaves are situated the ovules. These ovules are inserted on a special cellular body distinct from the carpellary leaf, which has been called the *placenta*,[1] the situation and arrangement of which in the ovary constitutes *placentation*. As a placenta exists on each of the two borders of the carpellary leaf, it follows that it is a double organ, though the two are

---

[1] *Spermaphorum*, *Colum*, or *Trophospermium* (Richard).

frequently coalesced into one. Hence it happens that the placenta is either two-lobed or made up of two diverging lamellæ; hence,

Fig. 249.—*Campanula Rapunculus*, L. Flower divided longitudinally to show the axillary pendent placentas, and the hairs on the style.

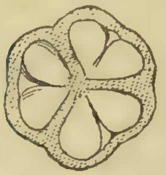


Fig. 250. —Transverse section of the fruit of a Hyacinth (*Hyacinthus*), showing axillary placentation and false dissepiments.

Fig. 252.—Transverse section of a Gooseberry fruit, to show the insertion of the seeds on two parietal placentas.

Fig. 251.—*Iris Germanica.* *a* Complete flowering plant, showing the petaloid styles, the rhizome, &c. ; *b* Transverse section of ovary, showing axillary placentation.

also, the ovules are often in two longitudinal rows. If the pistil consists of a single carpel, then, of course, there is only one placenta in the ovary. When the ovary is plurilocular, the placenta, which results from the coalescence of two marginal placentas, is situated in each loculament at the angle formed by the union of the two sides of each carpellary leaf. (1.) Such a placenta is said to be *axillary* or *axile*, the placenta meeting at and occupying the centre of the ovary. *Ex.* Iris (fig. 251 *b*), hyacinth (fig. 250), pear.

Schleiden, and, following him, Aug. St Hilaire and Payer, look upon axillary placentas as proving that the placenta must be a prolongation of the axis, as the ovule is a bud, and a bud can only be produced on an axis, not on the edge of the leaf. But, as we have seen (p. 181), it is a habitual character of various plants, and an occasional one of others, to produce such buds; so that we coincide in the opinion of the majority of botanists that the theory mentioned rests on very unstable ground.

(2.) Again, when the carpellary leaves which enter into the composition of an ovary are united by their edges, so that they form a unilocular ovary, though in reality of several carpels (p. 352); or when the carpellary leaves are folded upon themselves, but still do not form complete dissepiments,—the placentas are placed on the walls of the unilocular ovary, or on the edges of the incomplete dissepiments (fig. 252), as in the poppy, caper, rock-rose, violet, sundew, currant, and gooseberry orders, &c. Such placentas are *parietal.* In the *Hypericaceæ* (St John's Wort order) and *Cucurbitaceæ* (Gourd order), every gradation is found between axile and parietal placentation. It necessarily follows that an ovary with parietal placenta must be unilocular, unless (as in the Cruciferæ and *Tecoma radicans*, or trumpet creeper) the ovary is divided by false dissepiments (p. 352). Parietal placentæ are, like the placenta of a simple ovary, or of each carpel of a compound ovary, necessarily double, "but with this difference, that in these the two portions belong to the two margins of the same carpel; while in parietal placentæ they are formed from the coalescent margins of two adjacent carpels."[1] (3.) Lastly, the placenta may be *free central—i. e.*, forming a column in the centre of the ovarian cavity without any connection with the margin by means of dissepiments, as in common loosestrife (*Lysimachia vulgaris*, fig. 253), and the primrose, purslane, and pink families generally, where it is evidently due to an obliteration of the dissepiments;[2] or in the

[1] Gray, lib. cit., 293.

[2] Duchartre considers that in the *Primulaceæ* and *Myrsinaceæ* the placenta is truly and primitively central, while in the Caryophyllaceæ (pinks, &c.) it is originally axile, and only becomes free central by the obliteration of the dissepiments.—(Ann. des Sc. Nat., Nov. 1844, ii. 279-297, pl. vii. and viii.; and Revue botanique, ii., 1846-47, 213-225.) Cave (Sur le placenta libre des Primu-

Dionæa (Venus's fly-trap), thrift, &c., where it is a modification of parietal placentation, "with ovules produced only at the bottom."

Fig. 253.—*Lysimachia vulgaris*, L. (Loosestrife). A, Longitudinal section of the ovary, showing in the cavity circumscribed by the ovarian walls *fr*, the free central placenta *pl*, bearing the ovules *g*. B, Transverse section of the same ovary (same lettering as in A); *nv* indicates the limits of the carpels (mag. 5 times).

Abnormal Placentas.—In fig. 254 is shown the ovary of *Tamarix Africana* surmounted by three styles (*sl*), each terminating in a large blunt stigma (*sg*). At the bottom of this unilocular ovary we find several erect ovules (*ov'*) borne on a basilar process. This is not, however, a free central placenta. On examining it closely we find that this placentary mass is subdivided into three placentas, each of which corresponds to the median line of one of three carpels. In the closely allied genus *Myricaria*, we find these three placentas rising high enough along the median line of the carpels. We are therefore compelled to agree with Duchartre in considering this a parietal placentation, but obscure and abnormal on account of the placentas being on the middle instead of on the edges of the carpellary leaves.

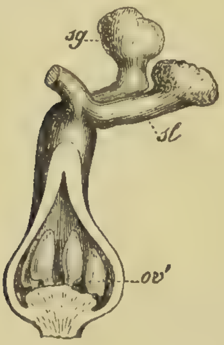


Fig. 254. — *Tamarix Africana*, Poir. Its pistil, with three styles, *sl*, part of one being cut away; *sg* Stigmas. The ovary has been opened longitudinally to show the ovules, *ov'*.

In the Nymphæaceæ, and more particularly in the white water-lily (*Nymphæa alba*), we find another abnormal placentation. As seen in the transverse section of the ovary on fig. 255, the ovules are attached to the numerous dissepiments which divide the ovary. In the Butomaceæ, in general, the carpels are not united into a compound plurilocular ovary, but it is on their lateral walls that the ovules are attached.

In the gourd and melon order (*Cucurbitaceæ*), there is an arrange-

---

lacées—Comptes rendus, lxx. 513-515) believes that the placenta is a prolongation of the stem.

ment of the placenta the nature of which has given rise to much discussion.

In fig. 256 is shown a transverse section of the ovary of the melon. The explanation given by the late Dr Lindley is that most generally adopted, and, so far as we are able to judge, most consistent with modern observations. According to him, these plants have three parietal placentas, of such a form that on making a transverse section of the ovary each of them resembles a mushroom, bearing the ovules under its large umbrella. These three bodies unite in due course in the centre of the ovary, in such a manner as to conceal their original nature. He thus considers the placentation of the Cucurbitaceæ parietal—a conclusion which the observations of Duchartre and others have only confirmed.

Fig. 255.—*Nymphæa alba*, L. (White Water-Lily). Transverse section of the ovary, already far advanced.

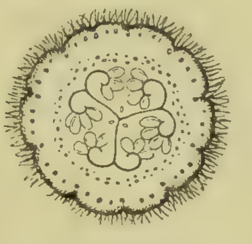


Fig. 256.—Melon (*Cucumis Melo*, L.) Transverse section of the ovary.

Parietal placentæ are sometimes so prolonged into the interior as to simulate true dissepiments, but they can always be distinguished from these by,—(1.) they are completely or almost completely covered by ovules; (2.) their placentæ alternate with the styles and stigmas, since the dissepiments correspond to and are opposite to the same stigmas.

The placenta varies in size. In the primroses, *Scrophularias*, &c., for instance, it is so large as almost to fill the whole cavity of the ovary.

Style.[1]—This is generally filamentous, and in shape cylindrical, though it may be triangular and other forms, and even, as in *Iris* (fig. 251) or *Canna* (fig. 198), petaloid. It is very often wanting—as in the poppies, *Chelidonium*, and *Platystigma*—when the stigma is *sessile* on the ovary. If the pistil is simple, then there is only one style, for a single carpel has but a single style; but if it is compound, then there may be as many styles as there are carpels entering into its

---

[1] *Tuba* of the old authors; plural, *stigmas* or *stigmata*, though the former is preferable, the word being almost Anglicised.

composition, as in the pinks. Thus in *Lychnis Githago* (corn-cockle) there are five. Again, they may be coalesced either for a part or the whole of their length. Thus, in *Malva* they are only united at their base; in *Geranium* the five styles are coalesced almost to their summit; while in the Belladonna, lily, &c., the styles are completely united into a single column. When the union between the styles is not complete, then the same terms are applied to express the extent of union which are used with reference to the leaves. Thus, when almost united to the summit, leaving only *two*, *three*, *four*, or a greater number of lobes, it is styled *bifid*, *trifid*, *quadrifid*, &c.; while if the union is for a less extent, leaving deeper divisions in the summit of the united styles, the terms *bipartite*, *tripartite*, *quadripartite*, &c., are applied. If, however, these terms are to be received as anything more than expressing the degree of coalescence of the styles, they are erroneous; for, as the student has already learned, the divisions at the apex of the style, and the divisions of the margins of leaves, are due to entirely different causes.

In some cases (*e. g.*, *Dictamnus* and *Biebersteinia Emodi*) the styles are united at their summits, but distinct at their bases. The styles may, as in the two plants last mentioned, be developed free, and get coalesced subsequently; or, as in the mallow, they are developed in a united condition. In the first instance they are called *styli coaliti;* in the second, *styli connati*. In Apocynaceæ and Asclepiadaceæ the stigmas alone are united.

(1.) The point of attachment of the style to the carpel is generally at the *terminal* point of the latter; but (2.), as in the strawberry and most other Rosaceæ, owing to the unsymmetrical development of one side of the carpel, the style may be *lateral*, or attached to the side a little above the base (fig. 257). (3.) Lastly, as in *Alchemilla*, *Soridium spruceum*, &c., it may be attached to the base, and is styled *basilar*. In such an ovary the style appears to rise from the receptacle, while in reality it arises from the lower part of the carpel. "In a pistil in which the styles are coalesced, the composite style which results from this union," to use the language of M. Achille Richard, "appears to spring directly from the receptacle; in reality, however, it takes its origin from the inferior part of the carpels." Such a form of receptacle has received the name of *gynobase*.[1] The loculaments of the ovary are swollen, so as to appear like a number of tubercles surrounding the base of the single style, which is consequently inserted lower than the summit of the tubercular-looking loculaments; hence such styles (*e.g.*, those of Boraginaceæ, Ochnaceæ, Labiatæ, &c.) are styled *gynobasic* (figs. 258, 259). The style may be (1.) *Caducous*, and fall shortly after fertilisation has been accomplished and the

---

[1] γυνή, and βάσις, base.

flower has faded (as in the cherry and the genus *Scirpus*). In this latter case it is not continuous with the ovary, but articulated to it.

Fig. 257.—Achene of the Strawberry, showing the lateral attachment of the style.

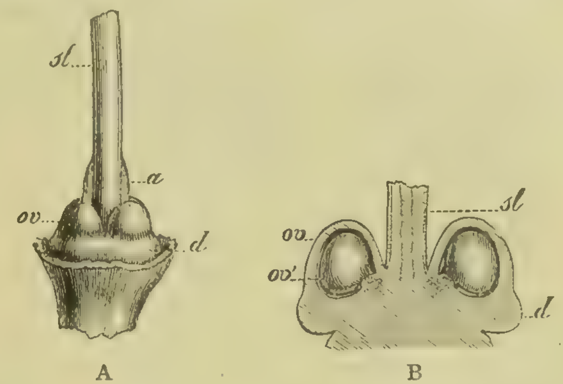


Fig. 258.—*Symphytum officinale*, L. A, Inferior portion of its pistil; *ov* Ovary; *sl* Style, which, at its base, forms two salient opposite angles *a*; *d* Disc (mag. 6 times). B, Longitudinal section, showing two open loculaments and part of the style (same letters as in the former figure); *ov'* Ovules (mag. 11 times).

(2.) It may be *persistent* and remain along with the fruit (as in the Cruciferæ); or (3.) it may be *accrescent*, and even increase after the flower has faded, as in Clematis, the anemones, particularly of the section *Pulsatilleæ*, &c., where it is plumose or feathery (Chap. X., FRUIT). Lastly, as Lindley long ago pointed out, *the style may be a process of the placenta*, "wholly free from the carpellary leaves, and not even guarded by an extension of their points." This is shown in *Babingtonia Camphorosmæ*, in which the style proceeds directly from the placenta itself, "and does not even touch the carpels, but is protruded through a hole in the vertex of the ovary." Something very analogous is seen in some species of the genus *Impatiens*. "In *Impatiens macrolula*[1] the style is surrounded below its apex by five points, which are evidently continuations of the backs of the carpels. These points are the points of carpellary leaves, which in such plants are separated from the placenta, and are merely pressed down upon it so as to cover the ovules, thus confirming the accuracy of the views concerning placentation held by Schykoffsky and Schlei-

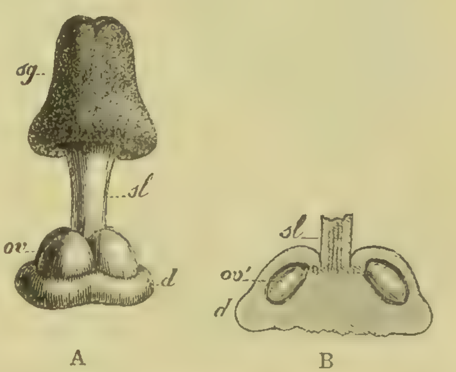


Fig. 259.—*Heliotropium Peruvianum*, L. A, Entire pistil: *ov* Ovary; *sl* Style; *sg* Very large stigma; *d* Disc. B, Vertical section of the ovary, and of the base of the style (same lettering); *ov'* Ovules.

---

[1] Botanical Register, 1840.

den. Upon that supposition the upper part of the style, and the stigmas, were assumed to be the naked apex of the placenta prolonged beyond the carpellary leaves. The consequence of that hypothesis was, that the conducting tissue of the style would be in most cases an extension of the placenta. That being admitted, the indusium (p. 361) of the Goodeniaceæ, and, *a fortiori*, the well-known rim found upon the stigma in Ericaceæ (heaths), would be the expanded end of the carpellary leaves, while the stigma of these plants is also the upper end of their placenta."

Stigma.—This is the glandular surface on the apex of the style; or, if the style be absent, it is sessile on the top of the ovary. It is uncovered with epidermis, and secretes a viscous material, which is usually most abundant at the period of fecundation. There are as many stigmas as styles, but the styles and stigmas may be separated or coalesced. If they are coalesced, they show on their apex a number of lobes equal to the number of styles and stigmas united together. Hence the stigma may be bi-, tri-, quadri-, or multi-lobed, or *bifid*, *trifid*, *quadrifid*, or *multifid*—or, finally, *bipartite*, *tripartite*, *quadripartite*, or *multipartite*, according to the extent of the union of the lobes (see also p. 358); or it may be simple—*i. e.*, without any divisions whatever. In such a case, it may scarcely be distinguished in size from the style, or it may be *capitate* or "headed," the head (*capitulum*) being *globose*, *hemispherical*, *depressed*, *elongated*, *subulated*, or of various other shapes. A simple pistil can have only one style and one stigma; but as the stigma corresponds to the margin of the apex of the leaf, this must also be double in its nature, as can be seen in the peony, tulip, &c., and in almost all cases in which the stigma extends down the inner face of the style. "Such unilateral stigmas," Gray most justly remarks, "we accordingly take to be the typical form, and say that, while the united margins of the transformed leaf, which compose the ventral suture, are *turned inward into the cell* (loculament) *of the ovary to bear the ovules, in the simple style they are exposed externally to form the stigma.* When the stigma is terminal, or occupies only the apex of the style, we suppose that these margins are unfolded in the style also, and form in its interior the loose conducting tissue through which a communication is established between the stigma and the interior of the ovary." The genera *Tasmannia* and *Schizandra* (Magnoliaceæ) are good examples of plants in which the stigma occupies the side of the ovary for almost its entire length.

Stigmatic Papillæ and collecting Hairs.—The surface of the style, stigmatic branches of the style, and stigma, may be smooth, or covered with papillæ, or, in the case of the former, with branched and plumose hairs, as in most grasses. In *Clarkia elegans* (fig. 260) the stigmatic papillæ are particularly well marked.

In some styles the hairs serve to catch the pollen which fall from the anthers, and accordingly have been called "collecting hairs." In the order Compositæ they are so constant and well marked as to form good characters for various groups. In *Campanula medium*, the collecting hairs, at first standing out from the surface like ordinary hairs, after a time get invaginated into sheath-like depressions on the surface of the stigma, taking along with them the pollen-grains (figs. 249, 261).

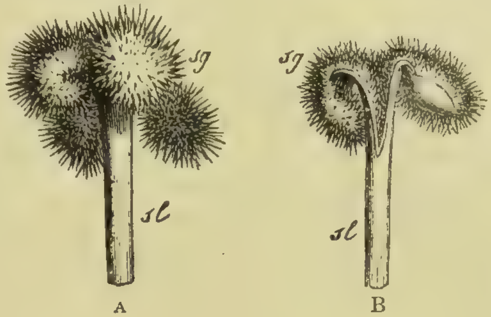


Fig. 260.—*Clarkia elegans*, Dougl. A, Extremity of the style, *sl*, and full-grown stigma, *sg*. B, Longitudinal section of the same, with the same lettering.

Indusiate Stigmas. — In fig. 261 is shown the stigma of *Leschenaultia formosa*, one of the Goodeniaceæ, which presents a structure more complicated than what we usually find in the stigma. In A, the style is shown as opening in the form of a sort of cup, or, as Robert Brown called it, an *indusium*, at the base of which is the true stigma, distinguished by the difference of its tissue. In some other plants of the same order, the indusium (B) has an entire margin. This arrangement of the stigma in the Goodeniaceæ favours fecundation. The five anthers are united in the form of an arch, under which lies the "indusiate" stigma. Accordingly, when the anthers dehisce introrsely, the pollen falls directly into the cup-shaped indusium, and there performs its functions towards fecundation.

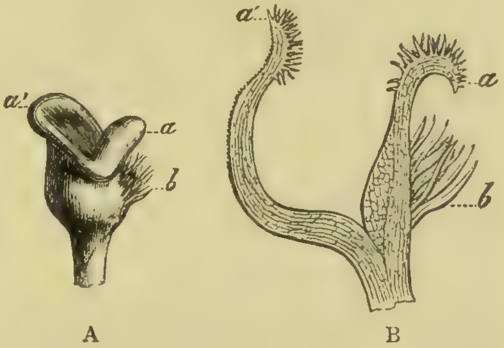


Fig. 261.—*Leschenaultia formosa*, R. Br. A, Extremity of a style expanded into an *indusium*, with two lips, *a' a*; *b* Tuft of collecting hairs (mag. 10 times). B, Longitudinal section of the same *indusium*, with the same lettering (mag. 20 times).

Stigmas falsely so called.—The term *stigma* is often rather vaguely applied in descriptive works; and though it ought to be limited to the secreting portion of the style, yet other portions of the style are so called. In the genus *Iris* the three large petaloid styles (fig. 251) in the centre are sometimes called stigmata, while in reality the stigma is confined to a narrow transverse humid space at the back of each style. In the Labiatæ, Bentham has shown that what is called a bilobed stigma is a bilobed style, the points only of the lobes being stigmatic: in the genus *Lathyrus*, and other leguminous plants, the hairy back of the style is often called the stigma; it is in reality, however, confined to the mere point of the style. In *Tupistra* the apparent stigma is a fungous mass, with a surface of the same nature as the style, in which no denuded or secreting surface can be detected. How the pollen acts on such a stigma so as to accomplish the act of fecundation is an interesting problem to solve.[1]

Structure and Formation of Carpels.—A *carpel* being only a modification of a leaf—indeed another form of it—has a very similar structure to that organ. It is possessed of an external and an internal epidermis, between which there is a more or less thick layer of cellular tissue, containing chlorophyll, and through which several vascular bundles permeate, in a direction from the base to the summit of the carpel, converging towards the style. Ordinarily, each bundle is perfectly distinct from each carpel in the ovary. These vascular bundles represent the nerves, and the inner and outer epidermis, the superior and inferior epidermal coverings of the leaf. Stomata are also frequently present on the outer epidermis of the carpels.

The *style* is originally composed of a more or less elongated tube, the walls of which contain false vascular bundles and tracheary vessels, which are a continuation of those of the walls of the ovary. The canal in progress of growth disappears, getting filled up with a loose, transparent, soft cellular tissue, through which the pollen-tubes descend to the ovule; hence it is called the *conducting tissue.*

The *stigma* is composed of elongated cells, closely packed together, and converging to the centre of the organ. In some cases these cells elongate into long cylindrical tubes with transparent walls, forming hair-like structures, more or less elongated (p. 360). It is entirely unprovided with epidermis proper, though, according to Brongniart, it is sometimes covered with cuticle. In general the stigma appears to be only an expansion superiorly of the conducting tissue. The stylary canal, except in rare instances (*Opuntia ficus-indica* and *Tropæolum*), does not open at the top of the stigma.

The *Placenta* is composed of loose cellular tissue pierced by vascular bundles, a branch of which goes to each ovule.

---

[1] Lindley, Introduction, &c., i. 369.

OVULE.[1]

The ovules are minute oval bodies, each of the average size of a pin's head, contained in the cavity of the ovary attached to the placenta, and which, when fecundated by the pollen, become the seeds. Before, however, becoming the seeds, the ovules have to undergo many changes; so that the structure of the ovule and that of the seed, though theoretically the same, are in reality very considerably different. The number of ovules varies from one in a simple pistil (when it is called *solitary*) to a great number. They are styled, when few and easily counted, *definite;* when in greater number, *indefinite.*

Development and Structure. — Its first appearance on the placenta is in the form of a minute tubercle, composed throughout of homogeneous cellular tissue, without any division in parts, and originating from a single cell of the placenta. Little by little there forms round the base of this cellular body a kind of ring or collar, at first in the form of a cup, this embracing the base only of the ovule, but by-and-by, developing by its free border, it ends by covering the greater part of the primitive tubercle. While this first envelope is growing, there is a second one forming at its base, and ending by covering it in a similar manner to that which the first envelope adopts in covering the primitive tubercle. The result is, the ovule is composed of a central cellular body covered by two superimposed envelopes, the one interior, the other exterior, pierced each at its summit by a large opening, by which the top of the primitive tubercle often protrudes in the form of a conical body. The centre body is termed the *nucleus;* the exterior membrane the *primine;* and the interior one, which is immediately laid over the nucleus, the *secundine.* The opening which occupies the summit of the primine is the *exostome,*[2] while that of the secundine is the *endostome.*[3] Such is the nomenclature of Mirbel,[4] and, as the most generally received one, we adopt it,

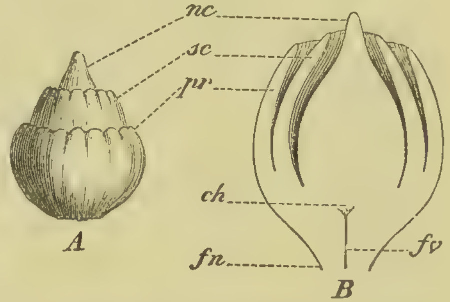


Fig. 262.—*Polygonum orientale*, L. Orthotropal ovule in two successive states of development. A, Entire young ovule. B, The ovule more advanced, divided longitudinally: *pr* Primine; *sc* Secundine; *nc* Nucleus; *fu* Funiculus; *fv* The vascular bundle, which terminates its course at the chalaza, *ch* (magnified 80 times).

---

[1] Latin *ovulum*, diminutive of *ovum*, an egg.

[2] ἔξω, without; στόμα, mouth.

[3] ἔνδον, within.

[4] Mirbel, Ann. des Sc. Nat., xvii.

though it possesses the anomaly of calling the first-formed coat by a term which would signify that it is the second in date (secundine), and the primine the first, though in reality it is the last formed.[1] Lastly, the term *micropyle*[2] is applied to the single opening at the summit of the ovule formed by the united exostome and endostome (fig. 263).

Chalaza, Hilum, &c.—These membranes coalesce at the base of the ovule in a single body, which gets the name of *chalaza;* while the term *hilum* is given to the point at which the ovule is inserted on the placenta. The ovule may be either sessile, or, as in many crucifers, &c., placed on a stalk (the *funiculus*, or podosperm[3]), which is simply a prolongation of the placenta. The vascular bundle (figs. 262, 263, *fv*) which enters the ovule does not penetrate the nucleus in most ovules, but terminates abruptly in the chalaza. In the ovule of the castor-oil plant, Cycads, Conifers, &c., according to Gris and Favre, the vascular bundle does not terminate in the chalaza, but spreads throughout the nucleus almost half-way up its length.

Relations of the Poles of the Ovules to each other.—The various coats of the ovules may maintain such a relation to each other that the micropyle is at the one end and the chalaza at the other, or they may be so twisted as to present the two poles in entirely different positions. The ovules, according to the relations which the different parts, and more particularly the different poles, bear to each other, have received various distinctive names. The chief forms are as follows: (1.) The *Orthotropal*[4] or orthotropous ovule. Here no change in the direction of the parts occurs in growth. The chalaza is the point of attachment to the placenta; at the opposite end is the micropyle: and the ovule is therefore straight and symmetrical. *Ex.* Buckwheat and various species of walnuts (Juglandaceæ), Myricaceæ, Urticaceæ, Cistaceæ, &c. (fig. 262). It is not a very common form.

(2.) The *Campylotropal* or campylotropous ovule.[5] In this form the chalaza and the hilum do not change their position, and the parts are superimposed in the orthotropal form; but it

---

[1] Thus Gærtner, and, following him, Robert Brown, have called the primine the *testa*, and the secundine (the *tegmen* of Brongniart) the *internal membrane;* while the primine (the *secundina exterior* of Malpighi) is the *integumentum secundum externum*, and the secundine the *integumentum primum internum* of Schleiden.

[2] μικρός, small; and πύλη, gateway or opening,—the *foramen* of Grew, the *ei-munde* of the Germans.

[3] πους, ποδος, foot; σπερμα, seed,—*nabelstrang*, or navel-string, of the Germans.

[4] ὀρθός, straight; and τρόπος, form: also called *atropous* (α, τρέπω, not turned) or *homotropous:* in German, *geradläufig.*

[5] καμπύλος, curved; in German, *krummläufig.*

grows unequally, the increase of one side of the ovule being more rapid than the other. The result of this is that it curves upon itself, so that the apex is brought close to the base (chalaza). *Ex.* In most Cruciferæ, Caryophyllaceæ (chickweed family), Solanaceæ (potato family), Chenopodiaceæ, &c. The common mignonette affords a good example.

(3.) The *Anatropal*[1] or anatropous ovule. Here we find the ovule, during the progress of growth, inverted upon its funiculus or stalk, so that, though it still remains perfectly straight, the positions of the base and of the apex are entirely reversed, the micropyle being where the normal position of the chalaza is in the orthotropous ovule, and *vice versâ.* Lastly, the funiculus adheres along the back of the ovule throughout its entire length, so as to form an elevated ridge, to which the name of *Raphe*[2] has been applied. Sometimes (as in the ovules of the *Magnolia*) the raphe is so coherent with the outer coat of the ovule as to be externally undistinguishable. *Ex.* This is the most common of all the kinds of ovules, and is well seen in the Liliaceæ, Ranunculaceæ, Cucurbitaceæ, &c. A good example is afforded by the common garden-plant, *Eschscholtzia Californica* (fig. 263), as well as by the apple, almond, &c.

(4.) The *Amphitropal* or amphitropous ovule.[3] This ovule may be looked upon as an anatropal ovule, in which the raphe only extends along the back of the ovule—only half-way from the chalaza to the micropyle—the result of which is, that it is attached to the placenta by the middle of one side. Between it and the anatropal form there is every gradation. *Ex.* Various Malvaceæ and Primulaceæ (mallow and primrose orders). Owing to the fact of such ovules standing with their axes at right angles to the funiculus, they are said to be *transverse.*

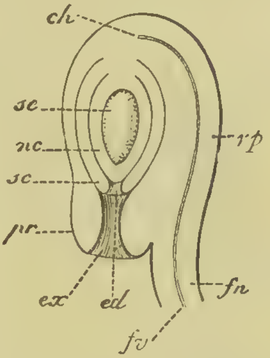


Fig. 263. — Longitudinal section of the anatropal ovule of *Eschscholtzia Californica*, Cham. *pr* Primine; *sc* Secundine; *ex* Exostome; *ed* Endostome; *nc* Nucleus; *se* Embryonic sac; *fn* Funiculus; *fv* Vascular bundle; *rp* Raphe; *ch* Chalaza.

In addition, some organographists distinguish *camptotropal*[4] ovules, which are curved like a horse-shoe, and each portion beyond the curve is of equal length, as seen in *Potamogeton;* and those called *Lycotropal,*[5] of a similar shape, but in which (as

---

[1] ἀνα, from above; τρεπω: in German, *gegenläufig.*

[2] ῥάφη, a line; or vasiduct.

[3] ἀμφι, around; τρεπω: also called heterotropal, hemitropal, or semianatropal.

[4] καμπτὸς, curved.

[5] λυκος, a hollow disc.

in a horse-shoe) the two branches on each side of the point of curvature are not united as in the former case.

Position of the Ovules in the Ovary.—The various positions and directions of the ovules in the cavity or cell of the ovary may be arranged as follows: (1.) *Erect*, when they rise from the bottom of the cell. *Ex.* Scabiosa or devil's-bit, buckwheat, &c. (fig. 262). In this case it will be attached to a "basal placenta," or a placenta at the bottom of the loculament (fig. 254).

(2.) *Ascending*, when they rise obliquely upward—from the side, a little above the bottom of the ovary. *Ex.* Buttercup.

(3.) *Horizontal* or transverse, when they project from the wall of the ovary in a transverse direction. *Ex.* Crassula.

(4.) *Pendulous*, when they hang from the upper part of the ovary in such a manner as to hang downwards in an oblique direction, as in the dandelion, sea-pink, &c. (fig. 264).

(5.) *Suspended*, when they hang perpendicularly from the very summit of the cell of the ovary. Ex. *Hippuris*, *Mycrophyllum*, and other Haloragiaceæ.

Fig. 264.—Longitudinal section of the ovary of the Sea-pink (*Armeria maritima*, Boiss.), showing the free central placenta in the form of a slender thread, from which the ovule is suspended (mag. 12 times).

When two ovules are placed side by side at the same level, they are *collateral;* if the one is above the other, they are *superimposed.* In either case, they may be situated the same as to the axis of the ovary, or differently; and the same rule is true when there are many ovules in a loculament.

These terms, as well as those referred to in the preceding paragraph, also apply to the seed.

Formation of the Tercine or Chorion.—Up to this period the nucleus of the ovule is a mass of cellular tissue. Gradually a cavity appears in the interior of this nucleus, which increases at the expense of the walls—these walls constituting a third membrane, which Mirbel has called the *tercine*, and Malpighi the *chorion*. This is sometimes described as possessing an inner lining (the *quartine*). The sac in the interior of the nucleus is the embryonic sac (the ammotic sac of Malpighi).[1] In the interior of the embryonic sac is the *germinal vesicle* (or primordial utricle, as it is sometimes called). It is found in the upper part of the sac, to which it is suspended by the *suspensor*,[2] and afterwards grows into the embryo or young plant. But this portion of the anatomy of the ovule will be best considered when we discuss the impregnation of the ovule (Chap. VIII.)

Exceptional Structure of the Ovule.—We have seen, from

---

[1] The *sacculus colliquamenti* of the older writers; the *quintine* of Mirbel; the *additional membrane* of Robert Brown.

[2] *Hypostasis* of Dutrochet.

the foregoing description, that the general structure of an ovule consists of a nucleus, most commonly conical, and covered by two superimposed membranes (primine and secundine); in the nucleus is a cavity (the embryo sac), in which develops the germinal vesicle attached to the top of the embryo sac by the suspensor, and becomes, after impregnation by the pollen, the embryo, or young plant in the seed. There are, however, some exceptions where the structure of the ovule is still more simple. In the ovules of the whole walnut family (Juglandaceæ), for example, there is only one integument covering the nucleus. A similar structure is found in the ovule of various species of *Veronica* (particularly *V. hederæfolia* and *V. Cymbalaria*), all the Betulaceæ (birch order), Asclepiadaceæ, Rubiaceæ, Labiatæ, Lobeliaceæ, Gentianaceæ, Boraginaceæ, Amaryllidaceæ, various of the Solanaceæ, Polemoniaceæ, Piperaceæ, all of the Coniferæ (except the genus *Podocarpus*, which has two ovular integuments),[1] and Caprifoliaceæ.[2] Indeed the majority of gamopetalous Dicotyledons have only one ovular coat. In the whole orders Santalaceæ (particularly *Santalum*[3]), Loranthaceæ (*Viscum*, *Loranthus*), *Thesium*,[4] Halorageaceæ (the common *Hippuris* or mare's-tail), and Balanaphoraceæ, there is a structure even less complicated; the ovules of these orders have only the nucleus without any covering whatever. The ovule of the coffee plant has only one envelope, forming, in this respect, an exception to the rest of the order Rubiaceæ. When only one envelope is present, it is generally looked upon as the secundine.[5]

Variation in the Number of the Integuments and the Form of the Ovules.—The rule that the form of the ovules and the number of the integuments remain the same in the same group is not without exceptions. Thus, among the Ranunculaceæ the genera *Clematis*, *Adonis*, *Aquilegia*, *Aconitum*, *Pæonia*, in addition to several species of *Delphinium* (*D. fissum*, *elatum*, *consolida*, *Ajacis*, &c.), have ovules with two integuments; while the genera *Thalictrum*, *Anemone*, *Hepatica*, *Ranunculus*, and, in the genus *Delphinium*, *D. tricorne* and *Chilense*, have only one integument to their ovules. On the other hand, the order Araceæ has in the genus *Calla* anatropal ovules, orthotropal in *Seuromatum*, and intermediate forms in other genera.[6]

Naked Ovules.—Exceptions to the rule that ovules are con-

---

[1] *Fide* Schacht.

[2] J. D. Hooker, Journ. Linn. Soc., ii. 163.

[3] Griffith, Linn. Trans., xix. 185.

[4] Decaisne, Ann. Sc. Nat., 2d ser., t. xi. 95.

[5] Before leaving this subject, however, it is proper to remark that Griffith (Linn. Trans., xix.) denied that *Viscum* has an ovule uncovered with primine or secundine.

[6] Schleiden, Beitraege, &c., 75-78; Duchartre, l. c., 595.

tained within the cavity of the ovary are casually presented by a few plants,—viz., the blue Cohosh of North America (*Caulophyllum thalictroides*), the ovules of which, rupturing the ovary soon after flowering, become naked; in the mignonette the ovules are also partially naked, the ovary being often at the summit, &c. In these plants, however, the ovules are fertilised in the ordinary way. In Cycadaceæ and Coniferæ there is, however, no ovary, each fertile flower consisting of an open carpellary leaf, in the place of a pistil, in the form of a scale. This scale bears two or more ovules on its upper surface, and the pollen is directly shed upon and fertilises these ovules without the intervention of a stigma and style, as in flowering plants proper. Hence these are called Gymnospermous or naked-seeded plants. In the firs, pines, &c., the above arrangement prevails; but in the yew the fertile blossom "consists of a solitary naked ovule, borne on the extremity of a short branch, and surrounded by a few bracts." In these plants there is, therefore, no carpel or pistil leaf at all.

Morphology of the Pistil.—From what we have already said, it will be seen that a simple pistil or single carpel is a single leaf, and that a compound pistil answers to several leaves united into a single body, just as several petals in a gamopetalous corolla, or several sepals in a gamosepalous calyx, are coalesced into one. On this view the carpel is the blade of a leaf, bent so that the opposite margins meet and unite, forming in this way a close case (the ovary): the under portion of the leaf will thus form the outside of the ovary, and the upper surface the interior lining of the same cavity. The ovules are borne on what corresponds to the united edges of the leaf, while the summit, "tapering and rolled together," forms the style. Lastly, the edges of the altered leaf, rolled outward at the top or along the inner edge of the style, form the stigma (p. 360).

The line formed by the union of the margins of the leaf is called the *ventral* or inner side *suture*, and always looks towards the axis of the leaf; while another line on the back of the ovary corresponds to the midrib, and, always looking outwards, is called the *dorsal suture*. The *placenta* is a cellular growth from the edges of the carpellary leaves. The *ovules*, on this view of the morphology of the carpel, are equivalent to the buds borne on the edges of such leaves as *Bryophyllum*, *Malaxis*, &c. (p. 181).[1] Numerous interesting observations confirm this view. In *Malaxis*, the buds produced in the margins of the leaves consist of a "flask-like cellular sac of a green colour, and within it and near its base a yellowish-green nucleus-like body. The cellular bag

---

[1] Hence the ovule is called by the German supporters of this theory "seed-bud" (samenknospe).

has a narrow opening at the apex, in some apparently bilabiate, in others slightly undulate,"[1]—a structure resembling the young axillary buds of one of its near allies—namely, the orchid genus *Microstylis*. This structure in the leaf-buds of *Malaxis*, Professor Dickie most judiciously points out as indicating the homology of the ovule to that of a bud, the nucleus-like body corresponding to an axis; the cellular open-mouthed sac he compares to an embracing leaf; the two coats of the ovule, when present, may be looked upon as homologues of two appendages (*i.e.*, leaves) on two consecutive nodes.

Finally, we may note that though the above view of the homology of the ovule—originated by Schleiden[2]—is very generally held, yet there are various other views adopted by several botanists whose opinions are entitled to respect. They may be briefly stated as follows: (*a*) That in most plants, and especially in Umbelliferæ, Ranunculaceæ, Leguminosæ, &c., the ovules are homologues of leaf-lobes (Brongniart, Godron, &c.) (*β*) That they are only metamorphosed leaves (Cramer). (*γ*) That they are comparable to the marginal glands of certain leaves. (*δ*) That the ovule may be compared to a phyllary expansion, the podosperm corresponding to the petiole, the outer coat to the leaf itself, while the middle coat is an appendage to the outer, and comparable to that which surrounds the nectary at the base of the petals in *Ranunculus gramineus*, *R. aconitifolius*, &c. (Lestiboudais). (*ε*) That ovules are leaf-buds in a particular state, and their integuments composed of scales of rudimentary leaves (Lindley)—a view slightly different from the generally received one. (*ζ*) Lastly, it is held that the ovules are the marginal lobes of a carpellary leaf transformed and convolute round the nucleus, which, being destitute of vascular tissue, is a "parenchymatous excrescence," or *trichome*, to use the German term. The primine, characterised by vascular bundles, is, according to this view, commonly the only membrane which persists in the mature seed. The secundine, except in rare cases (Euphorbiaceæ), is only a deduplication of the primine, and is mostly transitory.[3]

If the opinion which we have adopted regarding the morphology of the pistil needed to be supported by further argument, we might point out the case of the "double cherry," where the pistil loses its character of a carpel, and reverts to the structure of the leaf; to the observations of Professor Dickie upon several monstrosities of *Gentiana campestris*, in some of which the

---

[1] Dickie, Journ. Linn. Soc. (Bot.), xiv. 2 (1873); and ref. to Irmisch, Beitraege zur Biologie u. Morphologie der Orchideen, 1853, pl. iii.

[2] Acta Nat. Cur., xix. 1.

[3] Van Tieghen, Comptes rendus, Aug. 14, 1871; Ann. des Sc. Nat., Nov. 1872; and Le Monnier, Ann. des Sc. Nat., 1873.

ovary was transformed into a leaf, and the ovules into buds;[1] to the very similar observations of Henslow on the ovules of the mignonette; or to those of Schimper and Engelman[2] on various other plants. In willow flowers we sometimes find every gradation, from the true carpellary leaf back to stamens, until the retrograde development ends in true leaves. It must, however, be noted, in justice to those who take a different view of the morphology of the ovule, that the order of the development of bud-scales is different from that of the coats of the ovule, the inside scales in the bud being developed last—not the inside ones the first formed, as in the ovule; still the preponderance of facts is in favour of the generally received view which we have adopted.

---

[1] Trans. Bot. Soc. Edin., vol. iii.

[2] De Anthylosi Prodromus, § 44, 76, t. 5, fig. 4, 5. For a complete description regarding the theory of the carpel, &c., see Lindley, Elements, i. 369, 392; Chatin, Ann. des Sc. Nat. Bot., 5e ser., 1874, p. 5 *et seq.*, with references in that memoir to the treatises of Brongniart, Mirbel, Decaisne, Duchartre, Planchon, Barnéoud, Tulasne, Schacht, Rosanoff, Hofmeister, Robin, Chevruel, Duvau, St Hilaire, Baillon, and others, on the same subject (the structure and development of the ovule).

CHAPTER V.

DEVELOPMENT, PRÆFLORATION, SYMMETRY, AND METAMORPHOSIS OF THE FLOWER.

In this chapter we propose to consider briefly how the flower and its different parts are developed; how folded up in the flower-bud (Præfloration); a few particulars regarding the symmetrical arrangement of the different parts; and finally, Metamorphosis, or the changes from one part into another, which prove that every part of the flower is only a modification of the leaf, or of the leaf-type.

DEVELOPMENT OR ORGANOGENY.

Nearly all we have said about the leaf is equally true of the development of the flower.

Calyx.—This whorl appears first, and though in rare cases the separate sepals may unite, yet usually each sepal, in a dialysepalous calyx, is produced separately like a distinct leaf, and so remains; while a gamosepalous calyx is produced in the form of a ring, which subsequently forms the tube of the calyx. In the early stage of the development of the whorl, all the parts are regular; any irregularity occurs afterwards.

Corolla and Andrœcium.—The *petals* develop in the same way as the stamens, only a little later. The *stamens* appear later than the petals, yet develop earlier, owing to the retardation of the growth of the latter. The anther, on the other hand, will often be formed before the filament, and while the petals are yet merely embryonic. When once the corolla develops it grows rapidly, and encloses the organs lying within the whorl. The development of the petals differs from that of the calyx in the following respect—viz., that the base of each petal is frequently narrowed into a claw, which corresponds to the petiole of the leaf, and like it is formed after the blade; while in the calyx this claw, if present, is formed before the blade.

Each of the whorls of the flower shows itself in the form of little prominences, disposed in a circle around the axis. If these eminences grow in size without uniting, we have then a dialysepalous or dialypetalous calyx or corolla. But if they coalesce, then a gamosepalous or gamopetalous calyx or corolla is the result. The lobes of the calyx or the corolla correspond, in general, to divisions on the prominences mentioned, out of which these whorls develop.[1]

PRÆFLORATION.

All the different parts of the flower get packed in the flower-bud in various determinate ways, just as the leaves in the leaf-bud are packed after determinate methods (p. 162). A few words are therefore requisite regarding Præfloration, or Æstivation, as it is very commonly styled, Linnæus having applied this name to it, in contradistinction to *vernation*, applied to the leaves.[2]

We can study Præfloration from three points of view—viz. (*a*) Each verticil in particular, considered in reference to the parts which compose that verticil; (β) Each piece of the same verticil; (γ) Each verticil in reference to the position in which it lies to the other verticils. The study of præfloration, from any of these points of view, is often useful in the co-ordination of natural orders, as was long ago pointed out by Robert Brown.

1. General Præfloration of the Floral Envelopes.—There are two general ways in which they are arranged in the bud: (1.) *Superposition*, or one part being laid over the other in the verticil; (2.) *Juxtaposition*, when the borders of the parts in each verticil touch each other.

In Superposition.—The parts are arranged in a spiral, like the leaves on the branches, the petals, &c., being only modified leaves, though so closely foreshortened as to seem to be in a verticil. This is *spiral* præfloration; yet, according to the breadth of the parts and the extent of the superposition, it presents various modifications, and has received corresponding names.

(1.) *Imbricative*, where only the tops of the pieces composing the verticil touch (*Ex.* Corolla of *Camellia Japonica*, fig. 265).

(2.) *Convolutive*, when rolled round through almost their entire length (*Ex.* Calyx of *Magnolia*). In this case the outer pieces nearly entirely cover the inner ones, like convolute vernation of leaves (p. 163).[3]

---

[1] Martins, in Richard's Eléments, 203; Alex. Dickson on Development of Flower of *Pinguicula*, Trans. Roy. Soc. Edin., 1870; Masters on Development of Andrœcium of *Cochliostema*, Journ. Linn. Soc. Bot., 1872; M'Nab on Development of the Perigynium of *Scirpus*, ibid., 1873 (Ined.), &c.

[2] *Æstivus*, summer; *præ*, before; and *flos*, flower.

[3] This is, however, a most improper term to apply. We agree with Dr Gray.

(3.) *Quincuncial*, when there are two pieces wholly interior, two wholly exterior, and one (the third) with one edge covered by No. 1 on one side, while it covers No. 5 with its other side. Ex. *Geranium*, corolla of Rosaceæ, &c. (fig. 267.)

(4.) *Vexillary*, in the calyx and corolla of all true papilionaceous flowers, where the exterior petal or *vexillum* (p. 311) is the largest, and at first embraces all the rest. As nearly the same thing occurs in the violet, it is probably caused by some slight dislocation that takes place during the early growth of the organs in the irregular blossom (Gray), (fig. 266, D).

Fig. 265.—Opening bud of *Camellia Japonica*, L., var. *Chandleri elegans*, showing the perfect passage between sepals and petals, as well as imbricative æstivation. *a a a* Exterior leaflets, corresponding in appearance to sepals; *a'* Leaflets beginning to assume the character of petals, larger in size and reddish on their margins; *a"* A still more petal-looking leaflet; *b b b* Perfectly characterised petals, the last trace of the calyx-like appearance being gone.

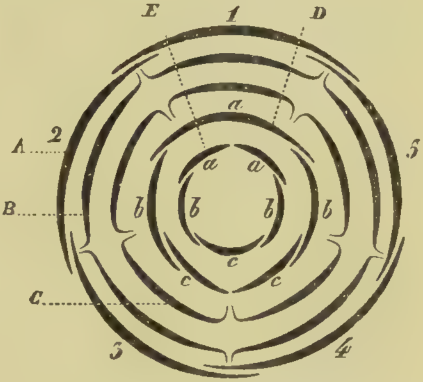


Fig. 266.—Diagram showing five different kinds of præfloration. A, Imbricative; B, Reduplicative; C, Induplicative; D, Vexillary; E, Cochlear.

(5.) *Twisted or Contorted.*—"In this mode, the leaves of the circle are all, or at least apparently, inserted at the same height, and all occupy the same relative position; one edge of each being directed obliquely inwards, is covered by the adjacent leaf on that side, while the other covers the corresponding margin of the contiguous leaf on the other side. This is owing to a torsion or twisting of each member on its axis early in its development; so that the leaves of the floral verticil, instead of forming arcs of a circle,

that it is practically inconvenient, and wrong in principle, to designate different degrees of the same mode by different names, and that it is to the *vexillary* mode of æstivation that the term properly applies. Long custom among descriptive botanists compels us, however, to use some of the terms in the ordinary way.

or the sides of a polygon, having for its centre that of the blossom, severally assume an oblique direction, by which one edge is carried partly inward and the other outward." It is rare in the calyx, but common in the corolla. *Ex.* Most Malvaceæ, St John's wort, &c. The term is often used interchangeably with "convolute."

(6.) *Cochlear*, in which one of the floral leaflets is large and rolled up like a snail's shell (*Ex.* Aconitum), only a modification of vexillary (fig. 266, E).

The foregoing terms also apply to the disposition of the sepals and petals in the calyx and corolla (dialysepalous and dialypetalous), and even when the sepals and petals are coalesced into one piece (gamosepalous and gamopetalous).

Præfloration by Juxtaposition.—There is only one essential modification—viz., the *valvate* form, in which each piece of the verticil comes in contact, edge to edge, through their entire length, yet without overlapping. Here all the pieces are arranged in an exact circle, none being lower or exterior, the edges being as thick as the rest of the organ, by which mark valvate præfloration may even be detected in an expanded flower.

There are, however, several modifications of valvate prefloration, which may be classed as follows: (*a*) *Induplicative* (fig. 266, C), in which the edges of the petals or sepals are bent in, or as in the calyx of *Clematis* rolled round, so that the flower, when cut across, does not present, in each piece, something like the arc of a circle. (*β*) *Reduplicative* (fig. 266, B), in which the margins of the sepals project outwards in the form of salient projections. In the corolla of many of the Malvaceæ, hollyhock, &c. (γ) *Open æstivation.* Lastly, in the mignonette, &c., the calyx and corolla are not closed at all over the parts of the flower in the bud, and hence this form of æstivation has been called "open."

2. Præfloration of each piece of the Verticil in particular.—Each part, when taken by itself, offers various positions, the nature of which it is well to know. For example, when the petals are irregularly plaited in every direction, as in poppies, they are styled (1.) *corrugated.* This points to a short calyx and a rapid growth of the corolla, for in very young buds there are no plaits on the petals. Some of the folds are inward, as in the corolla of the Gentians, and others outwards, as in that of the genus *Campanula.* Hence the streaks of colouring on the latter. In the bud of the Morning glory (*Convolvulus*), *Stramonium*, and many Solanaceæ, the pieces of each verticil are laid over one another in a convolute manner. Hence such verticils are said to be (2.) *supervolute.*

3. Relation of the pieces of the Verticil to those of the Verticil more interior.—If we examine a verticil relative to those in its vicinity, we observe two modifications: (1.) The pieces of the neighbouring verticil offer the same position; (2.) The pieces of two neighbouring verticils have different positions. For example, in *Parnassia* and *Elodea* the præfloration of the calyx and corolla is the same (quincuncially imbricated). In vines and Araceæ the divisions of the calyx, like those of the corolla, equally are in valvate præfloration. In Malvaceæ, Convolvulaceæ, &c., on the other hand, the calyx shows a valvate præfloration, while the petals are imbricated. It sometimes happens that the calyx is in a spiral, and that this disposition continues equally with the petals, as in *Magnolia*, *Nymphæa alba*, and generally in all those plants in which the sepals differ little from each other. In these cases we see that the first pieces of the second verticil follow immediately that which terminates the first, and follow then without interruption the spiral line commenced by the first verticil; while sometimes there seems to be a gap between the innermost sepal and the outermost petal, showing that something is wanting or abortive. Not only is there this arrangement between the pieces which form the two external verticils of the flower (calyx and corolla), but in some orders between the petals and the stamens which form the third verticil of the flower. Thus—*e.g.*, whilst in a small number of orders the stamens are opposite the petals (*Ex.* Rhamnaceæ), or in many others of those which are "diplostemonous" (p. 320), these are often concave or hood-shaped in form, and cover completely the stamens placed in front of them.

Præfloration of Stamens and Pistils.—The stamen, like the other floral organs, first appears in the form of little tubercles, which in general appearance differ nothing from those which afterwards develop into the sepals and petals. By-and-by, however, the part which in the former organs develops into the limb becomes the anther, and what remains as parenchyma in the leaf becomes the mother cells, which develop the pollen-grains (p. 344). Often the staminal whorl develops before the petals and sepals, as in the Grasses and Cruciferæ. In double flowers we see a transition between petals and stamens. The development of the pistil and its relation to the other parts we have already touched upon in the chapter treating of the Gynœcium. The stamens and pistils have, equally with the other whorls, determinate positions in the bud. Thus, in all the family of Urticaceæ—the nettle among others—the stamens are bent in the form of an arc, and curved toward the centre of the flower. An anomalous position may be remarked as existing in the carrot, parsley, and other plants belonging to the order Umbelliferæ. We there see that præfloration offers varied and somewhat important characters.

In order to examine these methods of præfloration—of which we have only given the barest outline, as the subject can be properly understood solely by referring to the plants themselves—the student should examine the buds just before they burst, as in a later condition of the flower the arrangements are totally effaced.

SYMMETRY OF THE FLOWER.

We have seen that the fundamental law which reigns in the flower is that the parts of the four verticils alternate one with another (p. 283), though it is not often that this perfect symmetry is realised. The parts of the flower may consist of two, three, four, or five sets of organs alternating with one another. In *Circæa lutetiana*, for instance, each verticil consists of two parts, and these regularly alternate with each other. In *Sisyrinchium*, and other Iridaceæ, the four alternate verticils are composed of three parts each. In *Isnardia*, and some other Onograceæ, four prevails; while in *Sedum rubrum* (fig. 267) five is the rule. Hence, to indicate the number of pieces which make up the different symmetrical alternating whorls, and to express the particular kind of symmetry, the terms *dimerous*,[1] *trimerous*[2] (figs. 269, 270), *tetramerous*[3] (fig. 268), *pentamerous*[4] (figs. 267, 271), according as two, three, four, or five pieces enter into the composition of each verticil, indicated by the symbols, $\sqrt[2]{}$, $\sqrt[3]{}$, $\sqrt[4]{}$, and $\sqrt[5]{}$.

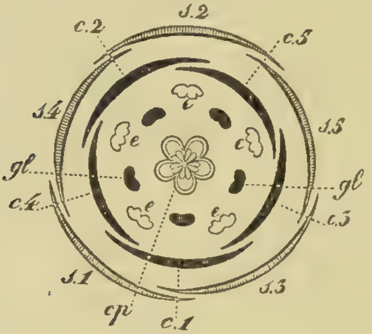


Fig. 267.—Diagram of the flower of a species of Stonecrop (*Sedum rubrum*, L.) *s* Calyx; *c* Corolla, both in quincuncial præfloration; *e* Andrœcium; *gl* Disk; *cp* Gynoecium.

Fig. 268. — Diagram of the flower of *Bunias*, DC., one of the Cruciferæ, showing tetramerous symmetry.

Variations and Alterations in the Symmetry.—In a great number of plants the exact symmetry is "disguised, masked, or

---

[1] δις twice; μερις, part.

[2] τρεῖς, three; the symmetry is sometimes styled *trigonal* (τρεῖς, three: γωνὶα, an angle).

[3] τετράς, four; sometimes the symmetry is called *tetragonal*.

[4] πεντε, five; also called *pentagonal*.

altered" by different causes, which we may indicate *seriatim.* These are :—

1. *Multiplication.*—In this case the number of parts entering into the composition of a verticil are increased beyond their normal number—this increased number of divisions forming two or more concentric verticils, alternating with each other. This is often seen in the andrœcium, as well as in the corolline and the other whorls. In the case of the stamens, when they become very numerous, they are apt to take the spiral instead of the verticillate arrangement. This is shown in the figure of the gynophore of *Magnolia grandiflora* (fig. 146, p. 287), the points where stamens are situated being indicated by cicatrices on the gynophore (*a*). In the water-lily (*Nymphæa*) all the whorls are much multi-

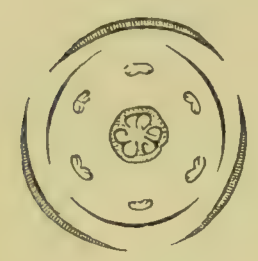


Fig. 269.—Diagram of the flower of a Hyacinth (*Hyacinthus orientalis*), one of the Liliaceæ.

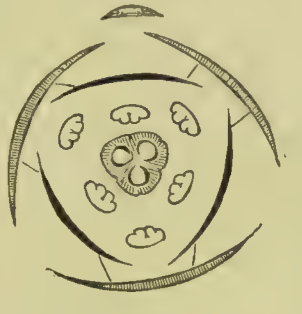


Fig. 270.—Diagram of the flower of *Muscari* (Grape-hyacinth), one of the Asphodelaceæ.

Fig. 271. — Diagram of the flower of *Myosotis palustris* (Forget-me-not), one of the Boraginaceæ.

Fig. 272. — Diagram of the flower of an *Iris*, showing trimerous symmetry. The three outer divisions of the perianth, with corolline appendages or hairs; three inner alternating; three stamens, and the trilocular ovary; the spathe is seen below.

plied. The sepals, petals, and stamens occupy numerous verticils. In the great division of Monocotyledons the normal symmetry of the flower is trimerous—*i. e.*, in threes, or multiples of threes (fig. 269); while in Dicotyledons it is *pentamerous*—*i. e.*, fives, or multiples of fives (fig. 267): and accordingly, though there are many exceptions to the rule, yet it may generally be concluded, when we find the corolla has a different symmetry than the above, that it is due to multiplication; or, when the parts are fewer, to the abortion of some members of the verticil. The multiplication of the members of a floral verticil does not necessarily interfere with the symmetry of the flower if the additional members are multiples of that which forms the basis of the flower, but it renders it difficult to be detected: and when, as in the case of the stamens, there is a great increase, the regularity is obscure or disappears.

2. *Chorosis or Deduplication*[1] is the division of an organ into a pair or cluster. This may be accomplished in two ways,—(1.) by *collateral* chorosis; (2.) by *vertical* or *transverse* chorosis. The first takes place when an organ is replaced by two or more situated on the same plane, the organs thus produced standing side by side. An example is afforded by *tetradynamous* stamens (p. 321) of the mustard and cress family (Cruciferæ).

In the case of *vertical* chorosis, the organs produced stand one before the other, as is seen in the "crown," or generally two-lobed appendage, on the inside of the blade of the petals of Silene (p. 313). Some stamens (*Larrea*, most plants of the Guaiacum order, and the Dodder) bear a similar but even more remarkable appendage. In both organs it may be looked upon as a "partial separation of an inner lamella from an outer," as the original theory of Dunal supposed was the case in the whole series of plants in which chorosis occurred.

3. *Coalescence*, or union of the parts.—This is so common that it is rare to find a whorl in which, to some extent at least, it does not occur. We have already fully considered it when discussing the gamosepalous calyx and the gamopetalous corolla, as well as the cases in which the stamens are united, either wholly or in part, to each other, or, in other words, become *monodelphous*, *diadelphous*, or *polydelphous*, &c. (p. 324).

The calyx of the common whin (*Ulex*) may be cited as a familiar instance of the symmetry of the plant being obscured by coalescence. At first sight the calyx of this plant appears to be composed of two portions almost entirely free,—an arrangement out of harmony with the law which prevails in these plants—viz., that the

---

[1] *Dédoublement* (*diremptio*, Lat.) of Dunal; literally, "unlining,"—the original hypothesis being "that the organs in question *unline*, or tend to separate into two or more layers, each having the same structure." Chorosis is from χώρισις, the act of separation or multiplication.

corolla is made up of five petals. However, on more closely examining the calyx, we find that one of the parts is terminated by two teeth and the other by three. We thus detect by means of these teeth that the calyx, like the corolla, is pentamerous, only that the five sepals are coalesced almost to the summit, on one side into two, and on the other into three—the five teeth pointing out the disunited tips of the five sepals.

4. *Arrest or defect in development.*—There is a frequent cause of irregularity in the symmetry of flowers by the abortion or suppression[1] of parts of the same verticil, or of another verticil alternating with it, or of several verticils of the same flower. Take, for example, tobacco, Belladona (in the order Solanaceæ), and we find five stamens alternating with five petals united in a gamopetalous corolla. Again, take the mullein (*Verbascum Thapsus*); one alone of the stamens which is placed between the two upper lobes of the corolla is much smaller than the others, owing to an arrest in development. Lastly, we may cite the flower of the snapdragon (*Antirrhinum*) as an example of the same irregularity. In the flower of this plant there is no trace of the fifth stamen, which has entirely disappeared. In the greater number of the Labiatæ (fig. 273) the calyx and corolla have a pentamerous symmetry, but the andrœcium has only four stamens; but we find that the fifth is abortive, and the place which it should have occupied is occupied by a vacant space. In such cases of natural abortion, we find that in all cases of monstrosity the wanting organ makes its appearance, thus pointing out what is the normal symmetry of the flower. Hence the value of the study of Teratology to the scientific botanist. In other genera of the same order, the sages (*Salvia*), for example, have only two stamens; but we have already seen that in these cases there remain traces of two stamens, and the general law which prevails in the order enables us to account for a fifth abortive one. Examples of abortion and suppression we have already considered in the case of various Primulaceæ,—in brookweed—*e. g.*, *Samolus Valerandi* (fig. 192, p. 313), where we find five scales (*e'*) placed precisely where we ought to have found five normal stamens, which have been aborted, so that the andrœcium is in alternating verticils; but by the abortion of one, the one which remains is opposite to the petals. Again, where we find, as in the primroses, all the verticils having a penta-

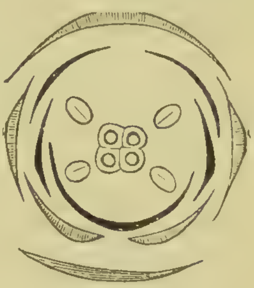


Fig. 273.—Diagram of the flower of *Teucrium Scorodonia* (wood germander), one of the Labiatæ.

---

[1] The term *suppression* is used when parts which belong to the plan of the flower do not appear in it; and *abortion* in addition to partial obliteration, as, for instance, when a stamen is converted to a scale or filament.

merous symmetry, except the andrœcium, which has the five stamens opposite to the petals, we are inclined to see in this a case of vertical chorosis.[1] Dr Gray also considers that *anteposition* or *superposition* of parts which normally alternate in the flower is not to be considered a case of transverse chorosis, and that the cases of the vine and buckthorn families, Linden, purslane, &c., can be explained in another way. "The position of the stamens before the petals in these cases, as well as that of the numerous petals in double camellias, arranged throughout in five vertical ranks, is most readily explained by supposing a return to the regular $\frac{2}{5}$ or five-ranked arrangement of leaves" (p. 184).

Lastly, an example of suppression has already been seen in *apetalous* plants (like the Chenopodiaceæ), where the petals are entirely absent, and the stamens therefore opposite to the segments of the calyx.

5. *The degeneration of the parts which form the floral verticils.*—We have seen, and when considering the subject of metamorphosis in the present chapter will consider the question more fully, that all the parts of the flower are only modifications of the leaf, and that frequently these parts return by regular gradations to the leaf, the pistils and stamens (as in double flowers) to petals, or even to true leaves, petals to bracts or leaves, and so on.

6. *Adnation or Consolidation* of the different floral verticils with one another.—This is seen in the familiar case we have already considered (p. 322), where one verticil or set of organs seems to grow out of another, as the corolla out of the calyx, or the stamens out of the corolla, or all of them out of the pistil, as explained when discussing the terms applied to such a union—viz., *hypogynous*, *perigynous*, and *epigynous* (p. 331); or where, as in the orchids, the stamens cohere with the style, or become *gynandrous* (p. 329). In the white water-lily, *Nymphæa alba*, a unique example is presented of the petals and the stamens being inserted on the walls of the ovary.

7. *Irregularity by unequal development.*—To all the foregoing causes of the disturbance of symmetry in the flower, we may add irregularity produced by the unequal development or unequal union of the different parts of the flower, though irregularity can also be produced by absorption or disappearance of some parts. A familiar example of irregularity produced by unequal development of certain petals is shown in the papilionaceous flower of the pea and bean order (Leguminosæ), already described (p. 311).

It is seldom, however, that any one of the foregoing interferences with the symmetry of the flower occurs alone. Generally two or more occur in the same plant; so that it requires the utmost care to detect the malformation, or to avoid being led astray by

---

[1] Schimper and Braun, Flora, 1839, p. 314.

the appearances which present themselves. Several of the deviations may even occur in the same natural order.

Primitive Regularity of the Flower.—Schleiden and Vogel showed that the papilionaceous flower, which is so markedly irregular, is in the bud quite regular; and Barneoud has since pointed out that it is a general law among all plants, and that in the early stage of the flower not only do they show a perfect regularity, but even present certain organs which disappear in the adult flower.[1]

Relation of the Floral Whorls to the Axis.—We have considered, when discussing phyllotaxis (p. 181), that the leaves describe certain cycles around the stem, and that, after each revolution, the next cycle commences exactly over the commencement of the former one, and so on. The material result of this is, that the homologous numbers are situated exactly over each other, and there must necessarily be as many vertical series as there are leaves in one cycle—*e.g.*, 2, 3, 5, 8, 13, &c. These series certainly appear more distinctly marked in some instances than in others, as Unger points out in a particular manner in the *Echinocactus* (p. 79, fig. 51), in which the perpendicular ribs of the stem are produced "by the interfusion of the superimposed leaf." In the flower where the members of the different cycles are simply modified leaves, a similar arrangement prevails, though not so readily seen. However, their case is different in this respect from the leaves—in so far that "even when only two similarly numbered leaf-cycles follow each other, as well as when dissimilarly numbered cycles are associated, there is never an uninterrupted progression. It is only in this way that, notwithstanding the crowded position of the leaf-cycles, the leaf elements in the flower do not cover each other. The measure of progression in the succeeding leaf-cycle is increased exactly so much that the elements of it come to be situated between those of the previous cycle, the consequence of which is an alteration of the leaves, which, as may readily be conceived, is not without its influence in the agreeable impression which the flower always produces in us. Thus, then, there presents itself in the flower, together with the greatest simplicity of elements, the most beautiful harmony in their arrangement, so that the architectural aspect of the flower becomes really a model of perfection in this respect; and, as the history of constructive art teaches us, it has always exercised a determining influence upon all the architectural works of man."

This simplicity is not, however, universally prevalent. In some cases, especially when the floral whorls are made up of a great number of parts, more complicated relations present themselves, as can be seen in the cactus, white water-lily, the *Calycanthus*

---

[1] Comptes rendus, 1846, t. xxiii. 1062.

flower, &c. Even in the flower of the latter the unity of design can be readily recognised. In fig. 274, A, is represented (after Unger) a vertical section of a flower and peduncle of *Calycanthus floridus*, and in fig. 274, B, a ground-plan of the same flower : *f* (fig. 274, A) indicates the origin of the true stem-leaves which have been removed ; *p* the coloured leaves of the envelope or perianth ; *st* the stamens ; *stab* the abortive staminal organs. In addition, there is represented at *m* the central substance of the peduncle, and *g*, the ovules situated upon its superior expansion.

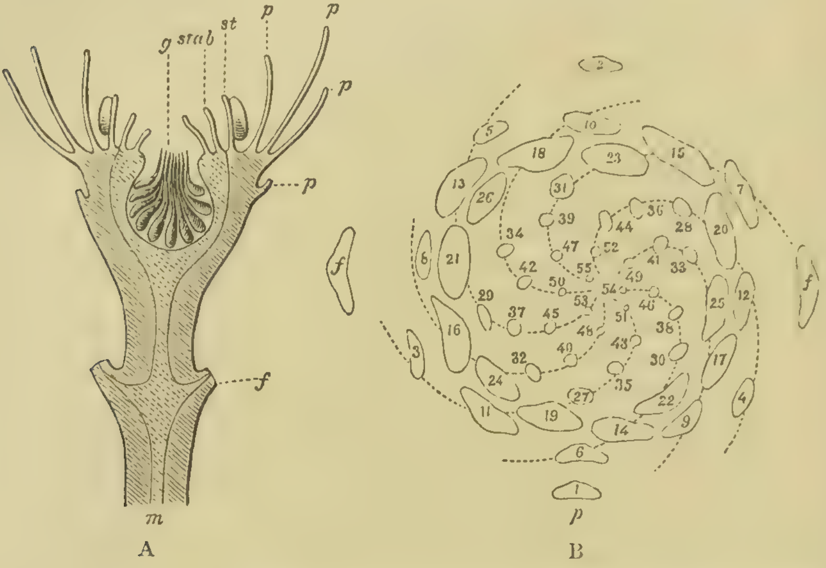


Fig. 274.—Longitudinal and transverse sections of the flower of *Calycanthus floridus*, DC. (Carolina Allspice tree).

In fig. 274, B, are shown the relations and position of the different parts in the flower. After the two opposite leaves *f f* there follow from 1 to 28, the leaves of the floral envelope (sepals of the calyx) at first reduced in size, then larger, and then again becoming smaller; after these from 29 to 41, the stamens (*st*) ; and lastly, from 42 to 55, the abortive staminal organs in the order pointed out.[1]

In order to study the relation of the floral whorls to the common axis, we should take the most external piece of the calyx as a point of departure, and then examine in what degree this piece corresponds to the axis, though placed semi-opposed to it. The same floral phyllotaxis, like the true phyllotaxis of the stem-leaves, is often followed out in all the genera of the same order.

---

[1] Unger, Botanical Letters (trans. by Dr Paul), p. 72.

METAMORPHOSIS OF FLOWERS.

When speaking of the different floral verticils, we have repeatedly pointed out that they are modifications of a single type, and that this type was *the leaf;* furthermore, that from the true leaf to bracts, from bracts to calyx, from calyx to corolla, and from corolla to stamens and pistils, there were in many cases regular gradations; and lastly, that in certain monstrous (teratological) conditions of the plant, any one or all of the verticils are liable to return to the true leaf-type. To trace all the floral organs as originating from and constituting modifications of one type, constitutes one of the most interesting sections of botanical study, and has served to rescue the science from being turned into a puzzling maze of names alone. Probably the earliest botanist who turned his attention to these questions was Joachim Jung, or Jungius, who in 1678 published at Hamburg a work on the subject entitled 'Isagoge phytoscopica.' The celebrated Linnæus—the father of the modern science of botany—did not neglect this department. In his 'Prolepsis plantarum'[1] he enunciated certain doctrines on the subject—rather crudely, it must be confessed. But it was not until 1759 that Caspar Friedrich Wolff, in 'Theoria generationis,' published anything like soundly philosophical views regarding the metamorphosis of the floral organs. His work abounds in errors, but it prepared the way for the ideas of a clearer-headed and more brilliantly philosophically-minded man than he—the celebrated German poet, dramatist, and naturalist, Johann Wolfgang Goethe, who, with the insight of genius, almost at once struck upon the real theory of the metamorphosis, as now held by almost every botanist.[2] Among the numerous writers who have advanced our knowledge of the subject of late years, De Candolle and Auguste de St Hilaire hold the first place; and though, doubtless, much specious theory and hypothesis which have got spun around it could be dispensed with, yet, nevertheless, the study of the metamorphoses of plants has thrown a flood of light on many obscure questions in systematic as well as in structural botany.

With this prefatory sketch of the history of research on the subject, let us call attention to a few of the leading points in this section of scientific botany. Having already touched upon all the main questions when describing the floral verticils, anything more than a brief outline is unnecessary.

---

[1] Amanitates Academicæ, vol. vi. (1763); Philosophia Botanica, 301.—"Principium *florum* et *foliorum* idem est. Principium gemmarum et foliorum idem est. Gemma constat foliorum rudimentis. Perianthium sit ex connatis foliorum rudimentis," &c.

[2] Versuch die Metamorphosen der Pflanzen zu erklären, 1790.

Transition from Leaves to Sepals and Petals.—Examine the white-flowered garden peony (*Pæonia albiflora*, Pall.), and there would seem to be the widest possible difference between the compound pinnatifid leaves of the stem and the ovoid white or rose-coloured petals of the corolla, perfectly simple in form, and entirely undivided on the margin, with the exception of a deep cleft at the apex of each. Nevertheless, a gradual transition from the one to the other exists. The inferior stem-leaves are of the normal type we have described; still higher up they are smaller and less divided; still nearer to the flower they become yet smaller, and present three undivided segments; higher still, the leaves, almost touching the calyx, present a single form with the limb undivided, and with scarcely an appreciable petiole. Then higher up, and forming the first row of sepals, are leaves still netted-veined, but with a broad sheath not prominently marked by veins, which in other more interior rows become the main portion of the sepal, the blade being only represented by a long narrow point at its apex. This point in its turn disappears, and a cleft in which it was situated alone remains, as in the petals. Thus we can trace the gradual change from the very unpetal-looking compound leaves to the petals themselves. In *Magnolia grandiflora*, represented in fig. 275, the calyx is composed of three sepals, which are so little different from the petals, more interiorly, that they are usually called *corolliform*. In *Camellia Japonica* (fig. 265) we also see a perfectly gradual passage from sepals to petals; and the same appearance may be seen in many flowers, those, for instance, of *Chimonanthus fragrans*, Lindl.[1]

---

[1] In some notes which a very intelligent observer—Mr Alfred Grugeon, Lecturer on Botany in the Working Men's College, Great Ormond Street, London—has favoured me with, he discusses the question of how little of the foliar leaf or appendages is represented in the floral organs of Dicotyledonous plants. "The chain of reasoning," he writes, "that suggests this problem is this—that though compound and stipulary leaves are prevalent in many orders in the foliar condition, yet we invariably come to simplicity in the floral. Now, the first question that presents itself is, what is it that disappears? If we take a thoroughly compound order like the Leguminosæ, we find the terminal leaflet to be the first to alter or absent itself, being represented either by a seta or a tendril; then another pair or two pairs become tendrils, or the leaf entirely disappears, and is represented by a phyllodium and stipules, as we find in many acacias, some species of *Lathyrus* and *Lupinus*. In the papilionaceous division of this order we find a pentamerous arrangement of the flowers, but irregular in form. And it seems to me that the vexillum represents the terminal leaflets of a compound leaf, which in all cases seems to reappear and assert itself in the flower. The wings and keel, from this point of view, would represent two pairs of leaflets, or perhaps one pair only and the two stipules. Taking this in conjunction with the inequality of the sepals and their position, the large sepal being opposite to the large petal would seem to indicate that the calyx and corolla were two compound leaves; and if we further carry out

Formation of Stamens and Carpels.—I. *Stamens.*—We have already traced the homologues of the leaf in the stamen (p. 336).

Fig. 275.—Entire flower of *Magnolia grandiflora*, L. *e* Mass of stamens; *p* Mass of pistils.

In the white water-lily (*Nymphæa alba*) the calyx is composed of four sepals, green exteriorly and white interiorly, a corolla of about eighteen petals, and numerous stamens in several rows around the pistil (fig. 276). The petals diminish in size from without inwards by regular gradations, until some of them are adherent to their tips on the internal aspects—a "little body, formed in general of two parts, adjacent and symmetrical," which it is easy to recognise as an anther (fig. 277, E). From this petal-like stamen there are regular gradations to the typical form of the stamen (fig. 277, E, G, H). In "double flowers," owing to changes in the constitution of the plant induced by cultivation, the stamens become converted into petals. The same monstrosity, however, occasionally occurs in wild plants, though usually in these cases all the

the investigation, we must consider the carpel to be the terminal leaflet of the next leaf, and the stamens to represent the two leaflets and stipules, equivalent to those that carry the keel of the corolla, which here becomes split up into shreds, although cohering more or less towards the base. This cohesion occurs also in the two petals from the keel. This theory was first suggested to me by finding a variety of *Trifolium repens*, known as *prolifera*, where there was retrograde metamorphosis which pointed that way. To turn now to the neighbouring order Rosaceæ, I think the reverse condition prevails in the foliar organs. We will assume this to be an order where compound leaves are conspicuous, as where they are simple they are always stipular. The simple leaf shows that, whatever else had disappeared, the terminal leaflet still remains. In addition to this, the terminal leaflet in the truly compound, and the terminal lobes of the divided though still simple forms, are always the most luxuriant."

stamens do not get converted into petals. Such flowers are *semi-double*. In most Monocotyledons, all the stamens except one are converted into petals ("petalised," as it is called). In a species of *Canna*, this single stamen preserves only a part of the anther, carried upon the edge of a petaloid filament, which is as vividly coloured as the other parts of the flower, and the style itself is also in the form of a brightly-coloured blade. In full double buttercups the inner petals have a tendency to become green; and a common monstrosity of the strawberry is for all the floral organs to revert to sepals or imperfect leaves of a green colour.[1] Sometimes a leafy branch will spring from the centre of the flower, or one flower out of the centre of another, as very commonly seen in roses. In this case the receptacle or axis of the flower assumes its ordinary vegetative growth, and instead of being surmounted by a rosette of floral leaves, gives origin to ordinary green leaves. Dickson[2] has noticed the conversion of bracts into stamens in a species of fir (*Abies excelsa*), a metamorphosis which Masters calls "staminody of the bracts."

Fig. 276.—Entire flower of *Nymphæa alba*, L. (White Water-Lily).

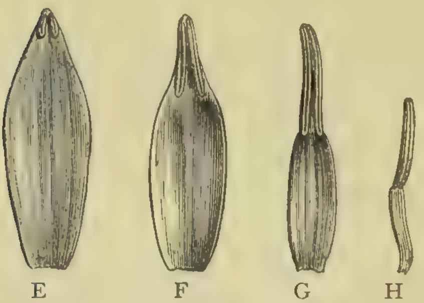


Fig. 277.—*Nymphæa alba*, L., series of forms through which the petals (E, F, G), each of which bears an anther, passes to the state of the normal stamen (H).

2. *Pistil.*—In most plants the pistil is not very leaf-like; yet in *Colutea*, *Stercularia*, &c., it is foliaceous-looking. In double flowers the pistil also frequently takes the leaf-like form, as seen in double-flowered cherry, &c. When the flower is entirely replaced by a tuft of green leaves, as mentioned in the preceding paragraph, the pistil is also transformed like the rest of the floral

---

[1] Duchartre, lib. cit., 443.

[2] Trans. Bot. Soc. Edin., viii. 60.

organs. Such flowers are sometimes called *chloranthous* (green-flowered).

It is from such facts as these that botanists are led to the irresistible conclusion that the leaf is the *type* on which all the floral organs are formed, and that they only differ from the ordinary leaves of the stem in their special development. In an early stage of their growth they all look alike. These organs have thus a tendency to *retrograde* metamorphosis, or to return to their original type either directly or to one stage of it, such as stamens to petals, petals to sepals, and so on. It must not, however, be supposed that the petal, though called a metamorphosed leaf, has ever actually been a green leaf, "and has subsequently assumed a more delicate texture and hue, or that stamens and pistils have previously existed in the state of foliage; but only that what is fundamentally one and the same organ develops in the progressive evolution of the plant under each or any of these various forms. When the individual organ has developed, its destiny is fixed."[1]

---

[1] Though the questions connected with the symmetry and metamorphoses of flowers constitute a most important section of botanical science, we have been forced, by the exigencies of space, to treat them very briefly. But even had we been able to do so at greater length, it is doubtful whether the student would have at this stage of his studies been benefited thereby. So much theory is mixed up with every question, that unless the subject is divested of this, and treated only in its barest outline, the tyro is apt to lose himself in the maze of mingled fact and fancy. The brevity of this chapter is the less to be regretted, because the subject is copiously treated, among others, in two books accessible to every student of the English language: Maxwell Masters's able work on Vegetable Teratology (Ray Society, 1869); and as regards American plants, in Asa Gray's Text-Book.

CHAPTER VI.

DISC AND NECTARIES.

In addition to the regular floral organs described in the preceding chapters of this section, there are in addition two *accessory* organs frequently present in the flower, which require notice before leaving the subject of floral anatomy. These are the *Disc* and *Nectaries.*

DISC.

This is a fleshy and glandular body found in certain flowers, but altogether independent of the four verticils described.

Position.—This is variable : sometimes it is found under the ovary and placed on the receptacle ; at other times at the bottom of the calyx, or on the summit of the ovary, in which latter case it is adherent to the tube of the calyx. In many cases it is a prolongation from the receptacle.

Position in reference to the Pistils or Carpels.—1. It may be placed under the carpels in the receptacle, when it is *hypogynous*, as in Cruciferæ, Labiatæ, snapdragons, Rues, &c. 2. It may be applied to the internal wall of a gamosepalous calyx, as in cherry, peach, &c., when it is said to be *perigynous*. 3. Or lastly, when the ovary is inferior, the disc is applied to the summit, and is *epigynous*, as in the Umbelliferæ, Rubiaceæ, &c.[1]

Effect of Disc on Symmetry.—Though not invariably present, yet when it is it has an effect on the symmetry of the plant, so that it may be looked upon as a fifth floral verticil. For instance, when absent, the carpels are, owing to the law of alternation, alternate with the stamens and opposite to the petals ; when it is present, these carpels are opposite to the stamens : so that in order

---

[1] In the Umbelliferæ it forms on the summit of the ovary a marked thickening, almost hemispherical, which appears to surround the base of the style as with a globe, and has received the name of *Stylopodium* (στύλος, style ; ποῦς, ποδὸς, foot).

to establish the normal symmetry of the flower, it is necessary, as Richard has shown, to regard the disc as a verticil interposed between the stamen and carpels (fig. 278).

Fig. 278.—*Vitis vinifera*, L. (the common Grape-Vine). *a* Fruiting branch, with *b*, the tendril; *c* Flower-bud; *d* Section of pistil showing the bilocular ovary with two upright ovules; *e* Flower showing the caducous petals united at the apex and separating at the base, with the disc surrounding the base of the ovary; *f* Andrœcium and gynœcium, with the small almost entire calyx, and the disc. The corolla has fallen.

NECTARIES.

Linnæus first applied the name nectaries to the glands which secrete a sugary substance in various flowers, and which attract butterflies and bees to these flowers. Afterwards, however, he extended the name so as to apply to all accessory portions of the flowers—*i.e.*, which did not belong to the calyx, corolla, stamen, or pistil, even when these organs or accessory parts did not secrete any honey-like substance. Hence considerable confusion has arisen as to the exact application of this term.

If the term is to be kept up at all, it ought to be reserved for the mass of glands situated in the interior of the flower, and which serve to secrete a honey-like liquid or nectar, and not to be confounded with the different kinds of discs, which are never secretory organs.[1] This has been done by Kurr,[2] and the idea has been carried still further by Caspary, in a special work he has written on the nectaries, who designates under this name, not only the glandular organs in the flowers, but even those in the petioles, stem, stipules, &c.

---

[1] Payer—one of our best authorities on the flower—for instance, styles the disc as the collection of nectaries taken as a whole, just as the mass of stamens was styled the andrœcium. Many authors (following Robert Brown) comprise, under the head of nectaries, the abortive stamens (or "parastamina") which are often found in plants, either under the head of antherless filaments, scales, little tubercles, &c. In *Persea Indica*, these rudimentary stamens are even more numerous than the fertile stamens, and simulate their position, nature, and appearance.—Schacht, Lehrbuch, &c., t. ii. 305, figs. 210, 211. Turpin proposed to use the term *Phycostema* to designate these "disguised" stamens.

[2] Uber die Bedeutung der Nektarien (1833).

CHAPTER VII.

THE INFLORESCENCE OR ANTHOTAXIS.

THE organs composing the flower and the leaves are morphologically the same, and the flowers are accordingly placed, like leaves, either at the end of the stem and branches, or along the axis. If we examine the Gentianella and the Pimpernel, we will find that the flowers are differently arranged on the stem, and are also different in their mode of development. The study of the mode, therefore, in which the flowers are attached to the peduncle, rachis, or axis of inflorescence, and the order in which they open (their evolution or *anthesis*), constitutes *anthotaxis*[1] or *inflorescence*. It is to the venerable Professor Röper of Rostock and MM. Bravais[2] that we are indebted for our first accurate knowledge of the various ways in which flowers are arranged; and the various terms applied to the inflorescence are in most cases of their devising. In the following pages we shall consider the subject, so far as our space will permit, from the stand-point of their original researches, and by the light which the recent studies of other botanists have thrown upon it. First, then, let us premise that a petal is morphologically a leaf—and a flower, accordingly, a collection of modified leaves, or a bud, but a bud which, unless in certain monstrous conditions (prolification) of the plant, terminates the axis on which it grows. Thus every axis is arrested by a flower, whether this axis is the main stem or one of its branches. If an axis is unbranched, then this is the most simple of all inflorescence—viz., a single axis with a terminal flower, as in *Gentianella*, Pimpernel, &c. If there is a flower in the axil of a normal leaf, then the stem is still simple, because there are only terminal leaf-buds and axillary solitary flowers. It differs, however, in this respect, that the elongation of the stem is capable of giving birth to many flowers, and in that the axillary flowers are primary, while the terminal ones are secondary in age. In the second case, the axis terminated by one flower is the peduncle.

General Division of Inflorescences.—We have already indicated that flowers are either axillary or terminal—that is, are

---

[1] *ανθος*, a flower; and *ταξις*, arrangement.

[2] Ann. des. Sc. Nat., ser. 2, t. vii. 193-291; viii. 11.

placed in the axil, or at the end of the axis. These are the two simplest ways of anthotaxis. In the first case, there is nothing to prevent the flowers being produced in indefinite numbers, the axis being always carried upward, and elongating by the terminal leaf-bud; while the flowers are produced in the axils of the leaf. Hence this is called the *indefinite* kind of inflorescence. In the second case, there is only one flower in the termination of the primary axis, which necessarily arrests the development of the axis in that direction; but if secondary, tertiary, or other axes are produced, then these may produce flowers—each of these axes, however, being terminated by a single flower, which, as in the case of the primary axis, arrests the development of the axis in that direction. This, then, is known as the *definite* mode of inflorescence. We must therefore study anthotaxis from these two stand-points separately.

First, however, let us further remark that in the *indefinite* inflorescence the *outside* or the *lower* flowers are produced first; and hence this kind of inflorescence is also known as *centripetal*, or "centre-seeking," from the fact that—as in a daisy, which comes under this mode of anthotaxis—the outside flowers are produced first, made first, or form the exterior towards the centre. In the *definite* inflorescences, on the other hand, it is the *inside* or *higher* flowers which are produced and fade first; hence this mode is known as the *centrifugal*, or "centre-flying," method of anthotaxis. The student may understand why in these inflorescences it is the outside *or* the lower flowers, or the inside *or* the higher ones, which are either produced or fade first or last, if we use Dr Maxwell Masters's familiar illustration: A daisy, or flower of that nature, we have already seen, consists of a number of flowers, all so crowded together on a foreshortened axis that they seem all together; and accordingly, if the axis on which they are placed was elongated, then the outside flowers will be below, and the inside ones higher up—just as if we suppose a coil of measuring-tape rolled up to represent the rounded or flat-topped inflorescence. If, however, you pull up the end which is the centre of the coil, then you will have the analogue of the long inflorescence; the outside coil, which was on a level with the inside ones in the former case, will now be below the inside ones by the elongation of that portion. A practical application of the nature of definite and indefinite inflorescences may also be given from the same source. For instance, when the gardener has to prune fruit-trees or roses, or thin grapes, take cuttings, or even cut flowers for a bouquet, if he cuts off the top of the wallflower, no more flowers will be produced on that shoot, because the wallflower is an *indefinite* inflorescence, and the gardener, by cutting off the terminal leaf-bud, has prevented the axis elongating in that direction. But, on the other hand, if the central flowers on a rose-bush are cut, then there will be still more left to "cut and come again," because the inflorescence of the rose is *definite*, and each axis terminated by a flower.

Again, in the indefinite inflorescence, the flowers are sometimes produced in the axils of leaves, or sometimes in the axils of bracts. Accordingly, the flowers placed in the axils of leaves follow the same disposition of leaves—viz., are alternate, opposite, or verticillate; or they may be pedunculated or sessile, or solitary, or in twos (geminate), threes (ternate), or fascicled (when there is a

Fig. 279.—*Juglans regia*, W. (Walnut). *a* Fruiting branch ; *b* Amentum of male flowers ; *c* Male flowers ; *d* Female flowers ; *e* Longitudinal section of a female flower ; *f* Longitudinal, and *g*, transverse sections, of the fruit (the so-called "tryma," a modification of the "drupe").

greater number than three), in the axil. The ways in which they are placed may therefore be described under the different kinds of inflorescence comprised under the head of *definite* or axillary, and distinguished by different names. Let us examine, then, first—

INDEFINITE, INDETERMINATE, AXILLARY, OR CENTRIPETAL INFLORESCENCES.

In this great division, the flowers of the inflorescence may be placed either on (1) primary, (2) secondary, or (3) tertiary axes or peduncles, or on the divisions of the last. We will describe them under their subdivisions.

(A) **Flowers on the Primary Axis.** — The inflorescences to be classed under this head are the *spike* and its subdivisions, the *catkin*, *spadix*, *spikelet*, *cone*, *capitulum*, and the *cœnanthium*.

1. *Spike* (spica). — Here we have a cylindrical and elongated central rachis carrying sessile flowers. *Ex.* The *Plantago*, or ribgrass (fig. 277). There are certain modifications of the spike dependent on the flowers being more or less sessile, and some of which often approach to the second class of indefinite inflorescences—viz., those on secondary axes. These are: (*a*) the *amentum* or *catkin*, in which we have sessile unisexual flowers — male or female — of which the male is articulated at its base to the rachis, and falls off in one piece after the plant has flowered, and in which the perianth is a simple scale. *Ex.* Hazel, willow, walnut, poplar, alder, &c.; hence called on this account Amentaceæ (figs. 279 *b*, 281).[1] (*β*) The *spadix*, or spathe, in which the rachis is a cen-

Fig. 280.—Spike of *Plantago lanceolata*, L.

Fig. 281.—Two small catkins of the American Hazel (*Corylus Americana*, Walt.)

---

[1] The development of the flowers of the hazel is curious. In the early part of the year, all that is seen in the female flower is two pink styles surrounded by a few scales, but without a trace of ovary or of ovules. These latter are not produced till nearly midsummer, and do not arrive at their full development till the succeeding autumn. M. Baillon has lately succeeded in tracing the

tral axis (generally fleshy) covered by flowers, unisexual and ordinarily *incomplete*—*i. e.*, they have no proper floral envelopes, but are covered completely by a large enveloping bract. The flowers are, moreover, not only sessile, but are embedded into the fleshy substance of the axis. This form of spike is only found in Monocotyledons, such as the cuckoo-pint, lords and ladies, and all Araceæ and palms. Most frequently in the spadix the female flowers are placed on the lower part of it, and the male ones higher up, with no interval between them, as in *Dracunculus vulgaris*, Schott, &c.; or, as in palms, each spadix may be unisexual, or diœcious, as in dates. The spadix may be either woody (palms) or fleshy (*Arum*). In palms the spadix branches often to a great degree, and acquires immense proportions—sometimes bearing as many as 20,000 flowers (fig. 154, p. 292). (γ) The *spikelet* of grasses is another variety of spike, and may be either simple or compound. In these plants the reproductive organs are made up of little inflorescences composed of several flowers attached along a common axis, the whole forming little spikes or *spikelets* (spicula, locusta). These spikelets, again, in their turn arrange themselves in various ways, most often in a raceme (as in *Bromus sterilis*, the barren brome-grass), or as in the common *Agrostis alba*, which is usually called in descriptive books a *panicle*, though Duchartre asserts that this cannot be properly applied to any inflorescence. At other times (as in rye-grass) the inflorescence is so arranged that it becomes a true branched spike, and in cultivated wheat the spikelets are arranged in a distichous order, one being placed in each "tooth" of the sinuous rachis, which

Fig. 282.—Extremity of a leafing and flowering branch of *Pinus Laricio*, Poir., bearing male flowers.

whole history of the development of these plants, which is remarkable not only for the great slowness with which it takes place, but also for the fact that the styles take precedence in their development over the calyx and involucre, as well as over the ovary.

is composed of scores of such teeth directly to right and left. (δ) The *cone* is also a veritable spike, in which the scales or bracts which accompany the female flowers are greater than those in the last-named inflorescences, and often woody (the male flowers, fig. 282, are borne on other branches). They are also persistent in most cases (though not in most species of *Picea*), and are not articulated at the base. *Ex.* Firs, pines, and other *Coniferæ*, or "cone-bearers" (fig. 124). (ε) The *capitulum*, or "little head," is a spike in which the primary axis is enlarged at the summit into a broad receptacle, on which are placed sessile flowers, united in a globose head. *Ex.* Sunflower, dandelion, daisy, and all other Compositæ (fig. 148). These inflorescences are surrounded by an involucre (p. 289), and the calyx is reduced to the state of a few hairs, which surmount the seeds in the form of a pappus (p. 300). The capitulum, then, is only an axis excessively depressed at its summit, and the flowers therefore appear to be in rows alongside of each other, the outer ones corresponding to the ones on the lower portion of the axis in the other forms of indefinite inflorescence; or the capitulum may be looked on as an umbel without peduncles. There are several kinds of capitula: (1.) the conical form, as in *Eryngium* (fig. 150, p. 289); and (2.) that seen in most other Compositæ.[1] The receptacle bears a number of *foveolæ*, or little pits, into each of which a flower is inserted. The central portion of the flower of a capitulum of the ordinary type is styled its *disc;* while the exterior portion or periphery is known as the *radius*. Lastly, we may mention that while in the petals of the greater number of flowers there is a median nerve which may be either free or anastomose with the neighbouring ones, in Compositæ there is either no such nerve, or if there is, it presents a singular modification. "In the monopetalous quinquedentate corolla of these plants we see five nerves which correspond to the five sinuses at the apex of the petal. Each of these, when they arrive at the base of one of the intervals between the teeth, divides into two branches, which direct themselves along the borders of each of them in order to reach the summit. In due time they terminate there, and, uniting in a single trunk, descend along the middle line, thus simulating a median nerve, but directed from above below, and not from below upwards, as is the usual way." Canini, in order to distinguish the mode of nervation in the petal's composition just described, applied to them the name of *Nevramphipetalæ*, or hairy "nerves around the petals." The capitulum may be compound, or, as in *Petasites*, there may be a raceme composed of capitula, just as other

---

[1] This L. C. Richard has styled a *cephalanthium* (céphalanthe), or "head of the flowers;" Mirbel, a *calathidium*,—words, however, of but little value or necessity in descriptive botany, and seldom used (except by their inventors). The enlarged receptacle has been also styled the *phoranthium* or *clinanthium*.

simple forms of inflorescence may, when compound, simulate in their mode of arrangement an entirely different inflorescence. (ζ) The *Cœnanthium*[1] is the general name applied to the peculiar inflorescence of *Dorstenia*, *Ambora*, and the common fig (*Ficus*). In *Dorstenia* (fig. 143) we see the receptacle very much enlarged, fleshy—somewhat quadrilateral, with the borders turned inwards and irregularly serrated—and the upper surface hollowed out in pits, in which are placed, intermingled, the male and female flowers. In *Ambora*[2] (a tree of Madagascar and Mauritius) there is an expanded receptacle, but much more concave. Lastly, in the fig we see the utmost extent of the concave development of the receptacle. In this plant the fruit (sometimes called a *syconus*) is pear-shaped, and the whole central cavity is filled with male flowers in its upper portion; while in the remainder, and greater

Fig. 283.—Fruiting branch of the Fig (*Ficus Carica*). *a* Fig cut longitudinally to show the collection of flowers inside the "cœnanthium;" *b* One of the staminate flowers; *c* One of the pistillate flowers; *d* Ripe fig (syconus) cut open to show the collection of fruits; *e* One of the fruits; *f* Seed with embryo.

---

[1] Nees v. Esenbeck, the *Hypanthodium* of Link.

[2] Belonging to the order *Monimiaceæ*.

part, are female ones—the receptacle having closed all around them, leaving only a small opening at the summit (fig. 280). Thus, while eating an unripe fig, we are in reality eating the fleshy receptacle and the whole inflorescence. Between the *capitulum* and the *cœnanthium*, as shown in *Dorstenia*, there is only a slight difference; and from *Dorstenia* up to *Ficus* the gradation is very gradual.

(B) **Flowers placed on the summit of Secondary Axes.**

Under this head we placed the *raceme*, *corymb*, *umbel*, and the so-called *panicle*.

2. *The Raceme.*—Here the main axis carries a secondary one all along it, as in the common gooseberry, the red currant (*Ribes rubium*), &c. It is such a characteristic form of the indefinite inflorescence that Guillard, in his treatise on the inflorescences,[1] proposed to designate the whole of the great division to which it belongs by this name (fig. 284).

Fig. 284.—The raceme.

Fig. 285.—The corymb.

Fig. 286.—The umbel.

In the *compound raceme* each peduncle may ramify several times, and thus produce a compound raceme (fig. 287). Generally the bottom branches are the longest; but sometimes the middle are so, giving it the appearance of the "thyrsus" of the Bacchantes. Hence this variety is often called a *thyrsus*—an indefinite and confusing term, as it is often applied to the inflorescences not only of the lilac (to which it properly applies), and to that of the horse-chestnut, which is conical, and even to designate inflorescences truly indefinite; while, on the other hand, De Candolle has transferred the name to designate inflorescences in which "an indeterminate rachis carries determinate floral groups."

3. *Corymb.*—If all the secondary axes of a raceme ascend to about the same height by the lower ones being more elongated than the upper, then the term corymb is applied to such an inflores-

---

[1] Bull. de la Soc. Bot. de Fr., iv. (1857) pp. 29-39, 116-124, 378-381, 452-464, 932-939.

cence. *Ex.* The hawthorn, &c. (fig. 285). In the *compound corymb* the peduncles are branches; and the pedicels, as in the simple corymb, though arising at different levels, terminate in flowers all

Fig. 287 —Fruiting branch and flowers of *Cinchona Calisaya*, showing the compound raceme.

more or less at the same level. A corymb is thus a shortened raceme; but in many Cruciferæ, such as candytuft (*Iberis*), &c., the inflorescence is a corymb elongated to a raceme, and called a *corymbose raceme.* The roses, pears, apples, and a family of Compositæ (*Anthemis*, *Arnica*, *Senecio*), &c., are called Corymbiferæ.

4. *Umbel.*—If the secondary axis or peduncles all arise from about the same place, and terminate on a level, then the term *umbel* is applied to the inflorescence (figs. 286, 288). It may, by the diminution of the rays (as in the cherry, primrose, &c.), be simple; but if the umbels branch, and form *umbellules*, then a compound umbel is produced, as in most of the Umbelliferæ, the parsley, carrot, anise, &c. &c.

(C) **Flowers placed on the summit of Tertiary Axes or their Ramifications.**

Under this head is usually classed the *panicle*, the *thyrsus*, the *compound corymb*, and the *compound umbel*.

5. The *panicle* is a term very generally used in books; but, as Payer truly observes, it cannot justly be applied to any characteristic mode of inflorescence. It is usually applied to a more or less compound raceme, as in grasses, but just as often to entirely different inflorescences, such as to a rachis, carrying numerous more or less unequal-branched peduncles, and accordingly should be dropped.

6. The *thyrsus* we have already shown to be a term which comes under the same category, and should equally be relegated to the crowded domain of botanical terminology, either obsolete or which deserves to be.

7. The *compound corymb* and the *compound umbel* we have already, for convenience' sake, described under the head of the simple corymb and simple umbel, though in reality they come under the present division.

Fig. 288.—Carraway (*Carum carui*), one of the Umbelliferæ. *b* One of the leaves; *c* Flower; *d* Fruit; *e* The two carpels of the fruit suspended by the columella (the fruit is a "cremocarp"); *f* Tap-root; *g* Flowering branch showing the compound umbel and umbellules.

DEFINITE, DETERMINATE, TERMINAL, OR CENTRIFUGAL INFLORESCENCE.

8. *Cyme* (cyma).—In the definite mode of inflorescence, as I have already pointed out, the axis terminates by a flower, which necessarily terminates and arrests its development. When the leaves are opposite, we find, at the base of the terminal peduncle, two opposite leaves, in the axil of each of which is produced a new peduncle, equally terminated and accompanied by two leaves, in the axil of each of which arise two lateral peduncles, the result of which is, that the inflorescence is composed of a series of superimposed bifurcations, in the centre of each of which there exists a terminal flower. Such an inflorescence is known as a cyme. If,

on the contrary, the leaves, instead of being opposite, are in verticels of three, each of them sending out a flowering branch from its axil, the result is, that there is a series of successive trifurcations. The first of these modes is called the *dichotomous cyme;* the second, the *trichotomous cyme.* An example is shown, among many other plants, in chickweed (*Stellaria*) and *Cerastium* (fig. 289). In the figure the entire inflorescence of the plant is shown.

Fig. 289.—Definite inflorescence of *Cerastium collinum*, Led. t Primary axis; t' Two secondary axes; t'' Four tertiary axes; t''' Eight quaternary axes; t'''' Quinary axes (cyme).

Here the primary axis t bears at its extremity, and is terminated by, a flower. All the inflorescence hinges upon this terminal flower. Lower down, however, there is an internode which bears two opposite bracts, from the axil of each of which springs a secondary axis, and these two axes comport themselves in exactly the same way as the primary one did—viz., they terminate by a flower; and a little below, from the axils of two bracts, they emit two tertiary axes, or axes of the third generation. These four tertiary axes in their turn behave exactly in the same way, giving origin to quaternary axes,—and so on. We also see this mode of inflorescence in the elder-tree (*Sambucus*), *Hydrangea*, &c.; but in some of these latter it is not always easy to detect the plan of the inflorescence, owing to the multiplicity and closeness of their bifurcations.

(α) *Dichotomous Cyme.*—We have already mentioned this term. *Cerastium collinum* (fig. 289) furnishes a good example of this form, which has also been called *biparous* by MM. L. and A. Bravais, and by others *alary* (*ala*, a wing), or winged, from the idea that the flower situated between the two symmetrical ramifications is like the body of a bird between its two expanded wings.

(β) *Trichotomous Cyme.*—In like manner, when, in place of bifurcations, the cyme forms trifurcations, then either the above term or *triparous* is applied to it,—and so on. Such cases are, however, rare.

(γ) *Monotomous Cyme.*—In some cases the dichotomy of the cyme continues regularly until it arrives at the last ramification, when one of the two lateral branches becomes abortive, as (*e.g.*) in *Cerastium tetrandrum.* When, as in the case of *Silene Gallica*, this abortion of the branch on one side becomes constant, the cyme thus produced has been called a *monotomous* or *uniparous* cyme.

(δ) *Scorpioidal Cyme.*—From the monotomous, then, we are led to speak of that variety of it called the scorpioidal cyme, as seen in all the plants of the order Boraginaceæ, such as *Myosotis palustris* (forget-me-not), in which the cyme is rolled round somewhat in the form of a crosier, or after the manner of a scorpion's tail—from which, indeed, it gets its name. In this form of cyme the flowers, arranged in a double row, only occupy the convex side of the curved or rolled axis, which is owing to the vigorous growth of the branches produced only in the axil of one dichotomous branch. Such a cyme has sometimes been called a *cincinnus.*

(ε) *Helicoid Cyme.*[1]—This form is much rarer than the former, and pertains to the Monocotyledons, *Ornithogalum*, *Phormium*, *Hemerocallis*, &c., and ought, according to Payer, to be defined as "an inflorescence in which all the flowers are of different generation, opposite, and disposed in a helicoid manner." In other words, it is much the same as a scorpioidal cyme, but with this difference, that the flowers and bracts, in place of being situated on the same side of the rachis, are arranged in a spiral, helicoid, or snail-shell fashion round the false axis—hence its name.

(ζ) *Contracted Cyme.*—Under this name De Candolle classed all cymes with very short peduncles. These comprise the *fascicle* (fasciculus) of Röper, where, as seen in the "Sweet-William," is a very compact cyme with "upright or appressed branches," though the term is applied by many botanists in an entirely different sense. The *glomerule* (glomerulus) is, again, a cyme so com-

---

[1] ἕλιξ, a spiral; and εἶδος, form: like a snail's shell.

pressed as to resemble a capitulum, from which, indeed, it is only to be distinguished by its centrifugal evolution. Lastly, the *cymule* (cymulus) is a diminutive cyme, or "a branch or cluster of a compound cyme."

Cymose inflorescence is often styled sympodial, and the cyme a *sympodium*—a term also applied to axes branching in this manner.

MIXED INFLORESCENCES.

The student will already have seen that it is by no means easy to accurately define some of the inflorescences, and that in nature they are even less distinctly divided from each other than in books. In truth, there are between many of them regular grada-

Fig. 290.—Flowering branch of the Castor-oil plant (*Ricinus communis*), with details of the male and female flowers, &c. The filament (*a*) is branched, each branch having a lobe of the anther ; *b* Female flower ; *c* and *d* Ovary entire, and in transverse section.

tions; so that while the main types are sufficiently well marked, an ingenious name-maker would have abundance of room for the exercise of his somewhat unhappy talent in devising designations for various others beyond those we have mentioned. Nor has the opportunity been neglected, as the "philosophical" classification devised by various botanists—chiefly German—prove; but these names are useless for the student's purpose, and have been deservedly neglected.[1] There are, however, a series of inflorescences, to which De Candolle applied the term "mixed," to which a few words must be devoted, as they comprise often the characters of both divisions of inflorescences — the definite and the indefinite. De Candolle ranged all these mixed forms under two great divisions—viz. (1.) Those in which an indeterminate rachis bears on its side determinate inflorescences. These he designates under the confusing name of *thyrsus*. (2.) Those in which a determinate axis bears indeterminate inflorescence. It is to these kinds that he gives the name of *corymb*, though the term is used by the best writers in a different sense. Payer mentions the following as examples of mixed inflorescences: (1.) The horse-chestnut, in which there is a raceme with *uniparous scorpioidal cymes*. (2.) *Chionanthes Virginica*, in which there is a raceme with *biparous cymes*. (3.) *Sparmannia Africana*, and, according to Payer, *Butomus umbellatus* (the flowering rush) also, in which there is an umbel of uniparous scorpioidal contracted cymes. (4.) In *Datisca cannabina* there is a spike of contracted biparous cymes with sessile flowers. (5.) In *Veronica centrifolia* there is a uniparous scorpioidal cyme in the form of capitula. (6.) Lastly, we may mention the umbel composed of biparous cymes, the raceme of biparous cymes, &c., as examples of mixed inflorescences.

Fig. 291.—*Euphorbia Canariensis* (in longitudinal section), the male and female flowers grouped in a calyciform involucre. The flower figured contains several male flowers and one female one, having three forked styles at the summit of the ovary. The flowers are naked, and the anthers of the staminate ones two-lobed (dithecal).

ANOMALOUS INFLORESCENCES.

Under this head Payer[2] has classed a number of inflorescences, such as when, in *Tilia* (fig. 147, p. 288) and *Helwingia rusciflora*,

---

[1] See Sach's Lehrbuch, &c. (1873, p. 509, &c.)

[2] Eléments de Botanique, 113-124.

the peduncle adheres to the bract through some portion of its length; the inflorescence of *Ruscus aculeatum* (p. 80, fig. 53); that of *Xylophylla obovata* (p. 81, fig. 54), in which buds are produced on the cladodia, &c. It has been argued that the flower of *Euphorbia* (figs. 290, 291), sometimes called the *Cyanthium*, is not a flower, but an inflorescence.[1] The latter view is, however, scarcely tenable. Many of these have been already described in an earlier portion of our studies; and with the others, which but rarely occur, and regarding the interpretation of which much difference of opinion exists, the student's attention need not be occupied at an early stage of his botanical instruction. It is enough to refer to them.

---

[1] For a discussion of the whole question see Dr Warming of Copenhagen's inaugural thesis—"Er Koppen hos Vortmælken (Euphorbia, L.) en Blomst eller en Blomsterstand? En organogenetisk morfologisk Undersögelse" (1871).

CHAPTER VIII.

FERTILISATION OF THE OVULE: ORTHOGAMY.

We have seen (Chap. III. p. 326) that the anthers open and discharge the pollen. This pollen is conveyed to the stigma either by falling directly upon it or by other agencies, which we shall duly consider in the next chapter. When the pollen-grains come in contact with the stigma, which is frequently moist, the grains do not burst, but the inner coat (endothecium) slowly projects through the outer one (exothecium) at particular points, such as the pores or slits in the outer, in the form of a long transparent tube, filled with the fovilla, which tube pierces the surface of the stigma (which is uncovered by epidermis), and penetrates through the loose "conducting tissue," which in the adult plant fills up the central canal of the style, until the tube reaches the mouth or micropyle of the ovule, when a mysterious operation is performed, necessary to the fertilisation of the ovules. After this fertilisation, the embryo or young plant grows in the ovule, and other changes take place which convert the ovules into *seeds* capable of reproducing the species. The process of impregnation or fertilisation may therefore be divided into three stages—viz. (1.) the preparatory or precursory phenomena; (2.) the essential process; and (3.) the consecutive changes. Let us consider this important function from these three points of view.

PREPARATORY PHENOMENA.

These commence with the opening of the flower, and in Compositæ and Campanulaceæ even before the flower has expanded. It is necessary that the pollen must have access to the stigma; and for this end there are various contrivances. In hermaphrodite flowers the stigma is often lower than the anthers of the stamens. In the fumitory family the stamens are placed in a close-fitting little sac formed by the spoon-shaped ends of the two inner petals, thus bringing the anthers close to the stigma. In the barberry, the anthers, when irritated by an insect finding its way into the flowers, spring up with force, and scatter the pollen on the stigma. The rapid growth of the stamen at the period of the opening of the flower is also favourable to fertilisation. In *Kalmia* and other plants, the stamens, when ready to discharge their pollen, gradually approach the stigma until they close over it. Very frequently, too, at the time the anthers are shedding their pollen, the surface of the stigma or stigmata exude a viscous liquid, which retains the pollen-grains after they have once come in contact with it.

Lastly, we may mention that in many plants the pollen is conveyed by insects, the wind, and other agencies, from one flower to another ; and that though in this chapter we shall describe the process of fertilisation as if the pollen of a hermaphrodite flower always fertilised the stigma of the same flower, yet it is known that this is by no means a general rule, as the remarkable discoveries of late years have abundantly proved. Whether, however, the pollen falls directly on the stigma, or is conveyed to it by other agency, the physiological phenomena are the same, and may be described preparatory to entering on a study of the various secondary ways in which the pollen is conveyed to those plants in which this *heterogamous*[1] fertilisation prevails, in contradistinction to those in which *orthogamy*[2] is the rule.

Among gymnospermous plants (pines, firs, and cycads), no ovary existing, the pollen falls directly on the naked and exposed ovules. In all other plants the ovules can only be fertilised through the stigma and style in the manner mentioned. The period of impregnation is also usually distinguished by the development of a higher degree of heat in the flower than is usual. [Sect. IV. HEAT.]

To insure fertilisation, there is, among other provisions, a large number of anthers and stigmas, and a superfluous quantity of pollen, in many plants. Morren found that in a single flower of the great-flowered cactus (*C. grandiflorus*) there are about 500 anthers, 24 stigmas, and 30,000 ovules. Each anther may contain about 500 grains of pollen ; so that in a single flower there may be as many as 250,000 pollen-grains. From the stigma to the ovules in this plant the distance is about 1150 times the diameter of the pollen-grain. It has been calculated by Mr Stephen Wilson that wheat-plants produce about fifty pounds of pollen per acre. In all other grasses, Coniferæ, &c., there is also more pollen than is necessary to fertilise the ovules, supposing that each grain took effect. In a single flower of *Maxillaria*, Fritz Muller calculated the number of pollen-grains to be 34,000,000.

---

[1] ετερος, crooked ; γαμεω, I marry.

[2] ορθος, straight ; γαμεω.

ESSENTIAL PROCESS.

The loose papillæ, hairs, or viscous substance on the surface of the stigma and style, serve to retain the pollen-grains after they have once reached the top of the stigma. On the stigma of the lily there is a notable amount of this viscous matter exuded. These grains absorb the moisture from the stigma, and then commence to grow or germinate—in other words, to protrude their pollen-tubes, which eventually reach the ovules. This is accomplished by the inner coat protruding through the thicker but more brittle outer coat. This takes place through the pores or slits; but if there are none (p. 343) on the pollen-grains, then the pollen-tube (or tubes) breaks through the outer coat at indeterminate places. Most frequently there is only one pollen-tube protruded; but it occasionally happens that there are two or more. In the pollen of Onograceæ, as many as twenty or thirty are sometimes protruded;[1] and in *Morrenia odorata*, so many are emitted as to give the head of the stigma the appearance of a mass of tow.[2] As a rule, also, no pollen-tubes appear at any place not in direct contact with the stigma. The inner coat, once it has protruded through the outer coat of the pollen-grain, lengthens into an attenuated tube, closed at the lower end, and filled with the fovilla or contents of the grain. It now penetrates between the loose cells of the stigma and the connecting tissue of the style, and appears at the placenta, or some other part of the lining of the ovary, when its end looks in appearance like a cell. The tube now enters the ovule at the micropyle, and therefore performs the fertilising process in the manner to be presently described. In gymnospermous plants the pollen-tube grows from the surface of the naked ovule; otherwise the process is exactly the same.

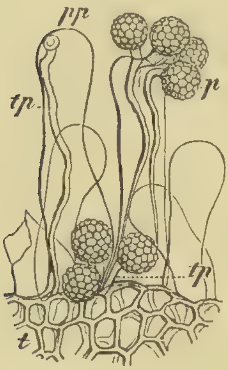


Fig. 292.—Longitudinal section of a fragment of the stigma of *Matthiola annua*, Sweet (the "ten weeks' stock"), showing some pollen-grains, *p*, which have emitted their tube *tp*. Several of these tubes have entered into the cavities of the stigmatic papillæ, *pp*; *t* Proper tissue of the stigma (after Tulasne) (mag. 163).

Usually each ovule has a single pollen-tube entering it; but in the beech, often in the Coniferæ, the crocus, *Ænothera muricata*, and the violet, the tube sometimes divides itself, so that one tube can fertilise several ovules.

Length of time taken to fertilise Ovules.—The time which the pollen-tube takes to penetrate the stigma and style varies in differ-

---

[1] Amici, Ann. des Sc. Nat., Nov. 1830.

[2] Lindley, Bot. Register, 1838.

ent species. In *Gladiolus segetum*, the style of which is four centimetres in length, the tube, according to Schacht, arrives in three days at the ovule.[1] In the *Colchicum*, Hofmeister found that the tube penetrated to the ovule in about from ten to twelve hours, though the distance to be traversed is about 9000 times the diameter of the pollen-grain. In *Tigridia conchifera*, Professor P. Martin Duncan calculated that the pollen-tube penetrated the style at the rate of one inch in four hours, and that under favourable circumstances it might be even less. In grasses, the time required is very short. In *Zostera* it is about 12 hours; in *Naias major*, about 24; in *Orchis morio*, 48; and in the greater number of Liliaceæ, Amaryllidaceæ, Iridaceæ, and Araceæ, it is much longer (Hofmeister). It is very dubious whether endosmosis setting in, owing to the moisture of the stigma, is the sole cause of the protrusion of this hernia-like tube. More probably the elongation of the tube is a true growth—like the elongation of a cell—and that it is nourished by the substance of the style, which it absorbs in its course to the ovule. This view is fortified by the fact that the tube elongates in some plants while the grains are still inside the anther—as, for example, in *Limodorum abortivum*, cypress, *Strelitzia reginæ*, and *S. angusta*. In Gymnospermæ, however, there is a liquid secreted by the integuments of the ovule, which seems to determine the issue of the pollen-tube from that part coming in contact with it.

We may also mention that (as shown in fig. 292) the pollen-tubes, *tp*, descend between the large salient cells which form the stigmatic papillæ, or even (according to Tulasne) penetrate into the cavity of these papillæ, and finally arrive at the fundamental tissue of the stigma. When (as in *Clarkia elegans*) the canal of the style opens in the centre of the stigma, the pollen-tubes enter without difficulty; but if, as is generally the case, the tissue forming the centre of the style is firm superiorly, the pollen-tubes, in penetrating the stigma, generally insinuate themselves into the vacant spaces between the cells. In some cases the pollen-tubes, in passing through the conducting tissue of the style, branch.[2]

Rate of Growth of Pollen-Tubes.—In some cases the pollen-tube protrudes almost immediately after the pollen has come in contact with the stigma. In other cases, it will not protrude for from ten to thirty hours, or even more, after the grain has fallen

---

[1] Monatsbericht, &c., 26th May, 1856 (*teste* Duchartre).

[2] By Decaisne and Gasparini it has been asserted that the emission of a pollen-tube is not always necessary to fertilisation; and so careful a botanist as Professor Dickie of Aberdeen (Ann. of Nat. Hist., vol. xvii.) has shown that in many plants the pollen-tubes found at the micropyle at the time of impregnation really originated there, and were not derived from the pollen. How these exceptional cases are to be accounted for on the general theory of impregnation, is difficult to understand.

on the stigmatic surface. In most cases the pollen-tube fades away with the stigma after it has arrived at the ovule and presumably performed its functions. In many plants, however, a long interval elapses between the time of the pollen coming in contact with the stigma and the fecundation of the ovules—for example, in the walnut and alder. In the former of these two trees the pollen falls on the stigma in February or March, and in the latter in June or July, but their fruit is not ripened until autumn. In most Coniferæ the ovule is not fecundated for a year or more after the pollen has been shed on it, the pollen-tubes seeming to remain inactive, but still living, during that period, in the conducting tissue of the style. Some of the Coniferæ, such as the junipers, take three years to ripen their seeds. In *Colchicum autumnale* the pollen falls on the stigma in the autumn, but it was not until the following April that Hofmeister could see any sign of the fertilisation of the ovule.

In any case, after the pollen-tube has penetrated the style and the stigma, the pollen-grain dries up, as does the stigma, the whole of the fovilline contents being then transferred to the pollen-tube, the lower part of which is in a growing state until it performs its function in fertilising the ovule.

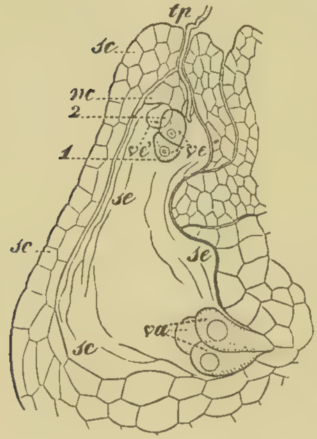


Fig. 293.—Longitudinal section of an ovule of the Garlick (*Allium odorans*) at the moment when fertilisation has begun to act. The promine has been suppressed. *sc* Secundine; *nc* Remains of the nucleus; *se* Embryo-sac; *tp* Extremity of a pollen-tube which has performed the act of fertilisation; *ve* Germinal vesicle fertilised and already subdivided into two cells; *ve'* Germinal vesicle not fertilised; *va* "Antipodal vesicles" (after Hofmeister).

The Embryo-Sac.—Before the pollen-tube has reached the ovule, or, even more commonly, before the pollen comes into contact with the stigma, the centre of the nucleus of the ovule, which has hitherto been a continuous mass of cellular tissue, gets hollowed out into a cavity, which gradually increases in size at the expense of its walls, until a considerable space is left in the nucleus near its apex. The walls of this cavity form the *tercine*,[1] or third coat of the nucleus, and the cavity itself is known as the *embryo-sac*, or, to use the term applied to it by Malpighi, the *sac of the amnios*. Most probably it results from the "special growth of a particular cell, which expands into a bladder or closed sac, at length commonly occupying a considerable part of the nucleus—sometimes remaining enclosed in its tissues towards its summit or orifice—sometimes displacing the upper part of the nucleus entirely, or even projecting through

---

[1] The "additional membrane" of the late Robert Brown.

the micropyle." It may be remarked, the embryonic sac does not always present itself in the form of a more or less swollen-out cavity—sometimes it is a slender tube stretching from the summit of the tercine above to the chalaza below.

It is in this sac that the *embryo*, or young plant, in the seed forms.

Origin of the Embryo.—*History of opinion on the subject.*—From the very earliest period since it was believed that there was some connection between the stamens and pistil of a sexual nature, it was also understood that the embryo was the product of the ovule, and was in some way fertilised or incited to growth by coming in contact with the pollen. The Greeks and Romans had some vague ideas regarding the two sexes in plants, observing that in order to produce fruit the pollen had to be taken from one date-tree, on which one kind of flower grew, to another, producing a different sort—the date being diœcious. Pliny knew that plants had different sexes, though he indicated no organs in which these sexes resided. In 1685, Grew admitted the existence of two sexes in plants, though Millington, Cæsalpinus, Malpighi, and others, have disputed the honour of this discovery with him; and in 1694, Camerarius published his views on the subject in a clear and explicit manner. From this time we may date anything like accurate ideas regarding the sexual differences in plants—the speculations of the medieval botanists being almost more vague than those of the Roman poets, Ovid and Virgil. In 1718, Sebastian Vaillant[1] published his opinion that the application of the pollen to the stigma was absolutely necessary, combating, however, at the same time, the view of Morland[2] that the pollen-grains traverse the style to the ovary and penetrate the ovules, substituting for it an infinitely more incorrect theory—viz., that it was only the vapour or volatile essence (" vapeur ou l'esprit volatil "), which, disengaging itself from the pollen-grain, fecundates the ovules. Passing over the singular, and singularly erroneous, views of Tournefort (which, however, found supporters in Siegesbeck, Heister, Schelver, who wrote as late as 1829, and did not believe in the sexuality of plants), we come to the celebrated Linnæus, who in 1735 published his 'Fundamenta Botanica,' who, in basing his classification of plants on the sexual organs, called anew the attention of botanists to their importance, and so gave a stimulus to the progress of research on the subject. Though Bernard de Jussieu in

---

[1] Discours sur la structure des fleurs, leurs différences et l'usage de leurs parties: Leyden, 1718. Sermo de structura florum; Paris, 1718. In Alston's Dissertation on the Sexes of Plants (Edin. Physical and Literary Essays, i. 228) is a history of embryogeny up to 1770.

[2] Philosophical Transactions, 1703 (xxii.), p. 1474; Acta eruditorum, 1703, p. 275.

1739, and Needham again in 1745, had observed the expulsion of the fovilla when the pollen-grains came in contact with moisture, it was not until 1822 that J. B. Amici,[1] of Modena, detected in *Portulaca oleracea* a pollen-grain emit the pollen-tube and enter the stigma and style; though in 1781 Gleichen, and Franz Bauer and Richard in 1811, had both seen, but did not divine its use in the economy of fertilisation. In 1826, Brongniart[2] clearly established the truth of Amici's observation, and the economy of the pollen-tube; though it is only of late years—thanks to the researches of many observers, and notably, Amici, Brown, Schleiden, Fritzche, Mohl,[3] Hofmeister,[4] Tulasne, Deecke, Schacht, Henfrey,[5] Radlkofer,[6] and others—that we have derived perfect knowledge regarding the passage of the pollen-tube through the style, and its uses in the fertilisation of the ovule, though on this little point our information would still bear improvement.

Function of Pollen-Tube.—At one time it was believed that the pollen-grain absolutely entered the ovule by the micropyle and became the embryo—an ingenious idea that was speedily abandoned. Then came the views of Horkel and Schleiden[7]—late professor of botany in the University of Jena—who held that *the end of the pollen-tube* entered the nucleus of the ovule and became the embryo. From the year 1837 up to a very recent date, this view was held by many botanists, among others by Schacht, Wydler,[8] Gelenzoff,[9] and Deecke,[10] but has now been completely disproved by the numerous observations of Mirbel, Brongniart,[11] Tulasne, Amici,[12] Herbert Giraud,[13] Mohl, Karl Müller,[14] Hofmeister, Schacht,[15] &c. Finally, the surviving eminent author of this theory, Dr Schleiden, and his most eminent supporter, Schacht, having themselves abandoned it, it would be a clear waste of time and space to give a *résumé* of the arguments either *pro* or *con*, but pass at once to

---

[1] Osservazioni mic. sopra varie piante, Atte della Soc. Ital. d'Scienze in Modena, xix. 23; Trans. in Ann. des Sc. Nat., ii. (1824) 64.

[2] Ann. des Sc. Nat., xii. (1827) 143.

[3] Ann. des Sc. Nat., ser. 4, t. 3, 1849, 1855.

[4] Vergleschende Untersuchungen der Keimung, Entfaltung u. Fruchtbildung höherer Kryptogamen u. der Samenbildung der Coniferen, 1851 (also Trans. Ray. Soc.)

[5] Trans. Linn. Soc., vol. xxii. (1856).

[6] Die Befruchtung der Phanerogamien, 1856, &c.

[7] Wiegmann's Archiv., 1837; Acta Nov. Acad. Nat. Cur., xix.

[8] Ann. des Soc. Nat., ser. 2, (xi.) 142.

[9] Bot. Zeit., 1843, 841.

[10] Bot. Zeitung, 1855; Ann. des Sc. Nat., 1855.

[11] Ann. des Sc. Nat., 1849, xii. 21-137; and 1855, iv. 65-122.

[12] Giornale Bot., 1840.

[13] Trans. Linn. Soc., xiv. 251.

[14] Ann. des Sc. Nat., 1848, p. 33.

[15] Bot. Zeitung, 1855; Ann. des Sc. Nat., 1855; The Microscope, in its special application to Veg. Anat. and Phys., trans. by Currey (1853).

the views which have displaced it. The almost universal belief among modern botanists is, that the pollen-tube—entering the ovule in virtue of some unerring but mysterious instinct (?)—terminates *on the surface of the embryo-sac,* though perhaps it may sometimes, under exceptional circumstances, and in particular plants, find its way into it.[1] However, this latter view has not been supported by observation of a trustworthy character. On the contrary, the pollen-tube has only been seen to become firmly adherent to the outer surface of the embryo-sac, into which, most probably by endosmose, the fovilline contents pass. After it has been emptied of its contents the tube withers away. In the meanwhile, the body out of which the embryo develops appears in the embryo-sac quite independently of the pollen-tube; though M. L. R. Tulasne (unsupported, however, by the greater number of observers) denies that it makes its appearance before the pollen-tube has entered the ovule and become adherent to the outside of the embryo-sac, and considered that the production of this vesicle is the first result of the influence of the pollen-tube on the embryo-sac. This body is the *germinal* or *embryonal vesicle.*

Germinal Vesicle.—The germinal vesicle, embryonal vesicle, or primordial utricle (for by all these names it is known), first appears on the upper part of the embryo-sac, near the place where the pollen-tube is applied externally, either loose or "adherent to the interior surface of the wall of the embryo-sac in the immediate vicinity, or sometimes separated from the embryo-sac by an interposed globule or by a pair of such globules," in the form of a simple cell, or rather a globule or mass of protoplasmic matter. This globule or cell insensibly elongates by the formation of transverse divisions, until, by-and-by, it constitutes a conferva-like tube. The cell constituting this is the *germinal vesicle,* which in due course takes on a rapid development; while the conferva-like tube, on the contrary, remains almost stationary, and forms what is known as the *suspensor* or suspensory cord.[2] If the pollen-tube did not reach the embryo-sac, and discharge its fovilline contents into it, the original little globule of protoplasm which forms the first trace of the germinal vesicle would progress no further. However, as soon as this is accomplished, the protoplasm takes a covering of cellulose on its surface, and thus becomes a true cell, and elongates into the tube already described. This elongated chain of cells (the suspensor) terminates, as we have already seen, in a single cell in no way different from the rest. By-and-by, however, while the other cells constituting the suspensor remain unaltered, this lowermost one divides in all directions, forming a

---

[1] Such exceptions Hofmeister described as occurring in *Naias,* passion-flowers, and some Geraniaceæ.

[2] *Hypostasis* of Dutrochet.

cellular mass, which increases and grows into the shape of the future embryo.[1] In Monocotyledons the development of the embryo is, up to a certain stage, the same as in the Dicotyledons, but with this exception, that when it arrives at that stage that the cellular mass must divide from the cotyledons or seed-leaves, only one is developed in the Monocotyledons, while two are produced in the dicotyledonous division of plants (figs. 294, 295).

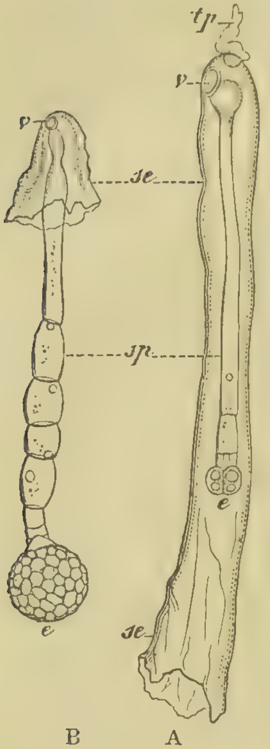


Fig. 294. — Development of the dicotyledonous embryo. A, First stage observed in the Dyer's Woad (*Isatis tinctoria*, L.) *e* Embryo; *sp* Suspensor; *v* Point to which it is attached to the wall of the embryo-sac (*se*); *tp* Extremity of the pollen-tube which has effected fecundation. B, State more advanced, represented after *Matthiola tricuspidata*, R. Br. (same lettering), after Tulasne. (A, mag. 150; B, 108).

The suspensor, which soon disappears after fertilisation, is always attached to the radicle end of the embryo, the cotyledons or seed-leaves occupying the other end. Hence the radicle is always directed to the micropyle of the ovule or seed.

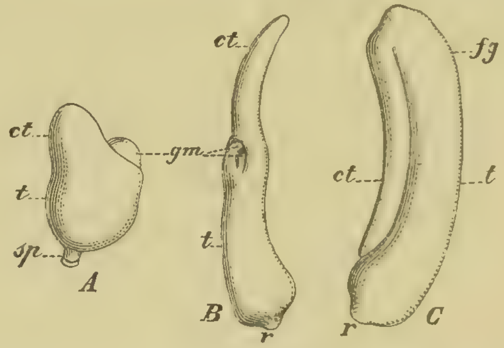


Fig. 295.—Development of the embryo of *Zannichellia palustris*, L. (Horned Pond-weed). A, Very young, showing the single cotyledon (*ct*), very short and large, embracing the portion of the embryo called the "gemmule" or bud (*gm*); *t* The "caulicle" or young stem; *sp* Portion of the suspensor. B, The same in a more advanced state (same lettering); *r* Radicular extremity. C, Adult state (same lettering). (A, mag. 90; B and C, 20.)

Sometimes there appear in the embryo-sac two or more germinal vesicles, which are fertilised, and develop into two or more embryos in the seed (as in the orange, mistletoe, &c.—See SEED, Chap. XI.) In firs, pines, and other gymnospermous plants, there are usually several embryos, though generally they all become abortive or rudimentary except one. In these plants (pines, firs, cycads, &c.) the embryo (among other peculiarities) does not appear until long after the pollen is applied, the embryo-sac being meanwhile "filled with cellular tissue, which forms the basis of

---

[1] This cellular mass, which afterwards becomes the embryo, Hofmeister called the pro-embryo (vorkeim).

the albumen of the seed." In these plants the embryo does not grow immediately within the single embryo-sac, but in particular cells which form within it, and which Robert Brown called *corpuscles.* "Each corpuscle in its turn produces in its interior a rosette of cells, generally to the number of four, with which the pollen-tube comes in contact. Then each cell of this rosette gives birth to a sort of filament of four other cells, placed end to end, very unequal in length, of which the upper has only a temporary existence, and the inferior one becomes the embryo by successive divisions and subdivisions."[1] We have already mentioned that all true pines mature their seed a year or more after that in which they have blossomed. Inside the embryo-sac is a fluid (the "amniotic fluid"), the function of which seems to be to nourish the young embryo.

In fig. 293 these facts are shown in a graphic form. In this figure the embryo-sac is already of considerable size; and as the embryo-sac increased, so the nucleus has diminished in an exact ratio. At the point where fertilisation operates we only see a few cells, *nc*, situated under the canal of the micropyle, and which are sometimes called by the French botanists *Mamelon nucellaire* or *Mamelon d'imprégnation* (*kernwaze* in German). The outline of the embryo-sac is designated by the letters *se*, placed on different points. In the midst of the amniotic fluid are seen several structures — viz., *va*, some extremely delicately-walled vesicles (which we have not hitherto spoken of), the use of which is unknown, and which only exist temporarily, disappearing soon after fecundation. They have been called *antipodal vesicles*,[2] so as not to prejudge their function. At the other end of the embryo-sac are the germinal vesicles (*ve*), which in the figure are represented to the number of two, placed side by side. The recent observations of Schacht seem to prove that in some cases at least the upper portions of the germinal vesicles are furnished with a singular cap-like covering, striated longitudinally, so as to appear as if covered with extremely delicate threads placed side by side. This he has called the filamentous covering,[3] and considered that it contributed to the fecundation of the germinal vesicle by communicating directly with the ends of the pollen-tubes—a view not generally held. Henfrey also saw them, but considered them due to coagulation. Schacht looks upon them as canals, while Hofmeister has

---

[1] Duchartre, lib. cit., 619; Robert Brown, Ann. of Nat. Hist., ser. 1, xiii. 368; Pineau, Ann. des Sc. Nat., ser. 3, xi. 83, &c. &c. The embryogeny of the Coniferæ is a subject yet likely to be fertile in discovery, as our knowledge of it is very imperfect.

[2] *Gegenfüssler zellen* of the German botanists. They were discovered by Hofmeister.

[3] *Fadenapparat* in German.

described them as a "secretion of the internal integument." In fig. 296 is shown a longitudinal section of a pistil, in which these facts are made out even more clearly.

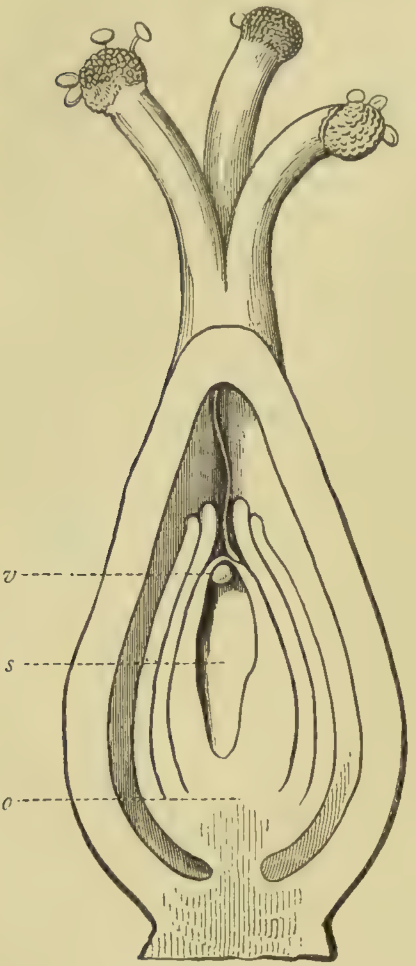


Fig. 296.—Magnified pistil of Buckwheat; ovary and ovule divided longitudinally; some pollen-grains on the stigmas; one grain distinctly showing its tube, which has penetrated the style, reappeared in the cavity of the ovary, entered the micropyle of the orthotropous ovule (*o*), and reached the embryo-sac (*s*), near the germinal vesicle (*v*). (After Gray.)

Résumé.—We have seen that the fertilisation of the ovules consists in (1.) the anthers opening, and the pollen-grains falling on the stigma; (2.) in each pollen-grain protruding either through the pores or slits, or through no determinate portion of the exothecium, one or more delicate short tubes, formed by the endothecium; (3.) these tubes, filled with fovilla, penetrate the stigma, and find their way, either slowly or quickly, through the connecting tissue of the style, until they arrive in the ovary; (4.) arrived in the cavity of the ovary, each tube penetrates into the ovule through the micropyle; (5.) they do not, however, enter into the embryo-sac, but adhere to the outside of the sac, into which, by endosmosis, each tube discharges its fovilla; (6.) fertilisation having been thus effected, the germinal vesicle appears—or, as many have considered, even before fertilisation—in the form of a little globule of protoplasm, which takes a coat of cellulose, then it elongates into a little chain of cells (the suspensor), the last one of which increases rapidly, until it takes the form of the embryo or future plant in the seed; (7.) lastly, the pollen-tube gets absorbed, and disappears. What is the mysterious vital function of the pollen-tube and its fovilline contents we know not.

CONSECUTIVE PHENOMENA.

The ovules fertilised, we may leave them, until we again have to consider them more fully as the *seeds*. Fertilisation is the aim and acme of the existence of the plant, to which all other functions are only subservient. Once this is finished the flower fades, and dies, and the petals fall off. The stamens, stigma, and style, though occasionally persistent, also generally fall too; but the ovary, being required to shelter the young seed, remains, and afterwards becomes the *fruit.* In the heath tribe there is an exception to the above rule, in so far that the corolla also persists; and if the ovary is "inferior" (p. 332), the ovary being intimately united to it, the calyx also remains behind, and forms a portion of the fruit, or ripe condition of the ovary. In the "winter cherry" (*Physalis Alkekengi*) we have already seen that the calyx, which is red in colour, survives fecundation, and forms the bladder-shaped covering usually taken for the outside of the fruit, which is in reality contained within it.[1]

---

[1] The history and literature of recent discoveries on fertilisation will be found in a paper in 'Flora,' 1857, p. 125. In addition to this, and the Memoirs referred to in the preceding chapter, the student should consult a treatise by Hanstein in 'Monatober. der niederrheinischen Ges. f. Natur—u. Heilkunde,' 15th July and 2d August 1869 (*teste* Sachs); and 'Botan. Abhandl.,' Heft i., &c.

CHAPTER IX.

FERTILISATION: HETEROGAMY.

In the preceding chapter we have considered the subject of the impregnation of the ovule, and fertilisation generally. For the sake of convenience, the typical method in which this function is performed has been taken as that of the stamens discharging their pollen on the stigma of the pistil of the same flower. We have seen that in hermaphrodite flowers this may be the case, if the flowers are "homogamous"—*i.e.*, if the stamens and pistils are ripe at the same time; but that in monœcious, and still more in diœcious plants, there is a difficulty in regard to the act being performed in this simple fashion. In the present chapter we will consider other methods in which impregnation is effected, and we shall find that, instead of this hermaphroditic fertilisation being the rule, as was until recently supposed, in reality facts are daily accumulating which would lead us to believe that in all probability it will soon be proved to be the exception; in a word, that even in plants where the stamens and pistils are in the same flower, it is rarely that the pollen from the stamens of that flower falls on the stigma of the contiguous pistil, and that even elaborate contrivances exist to prevent this.

Perhaps the most convenient method of considering this subject will be first to discuss the question of *Hybridity* in general, and then the different ways in which hybridity may be produced, either fully, as between plants of different species, or only between different individuals of the same species, both tending to the same end—the invigoration and perpetuation of the species,—a fact now tolerably well established, notwithstanding the noisy denials of some botanists of a school now happily almost extinct. These *circuitous* methods of fertilisation may be called *Heterogamy*, or "crooked fertilisation," in contradistinction to the typical and orthodox method, which may be styled *Orthogamy*, or direct ("straight") fertilisation.

HYBRIDITY.

When the pollen of a plant is used to fertilise the ovules of a closely-allied species by being scattered on the stigma of that species, the result is a plant springing from the seed so fertilised combining to some extent the qualities of both parents. This plant is called a *hybrid*, and corresponds to a "mule" in the animal kingdom. That this hybrid cannot, except in very rare instances, reproduce itself, and that a cross between species not related, except in a very near degree, is impossible, were until late years canons of faith among botanists. It was furthermore believed that the object of this hybridity, except among closely-allied species, and their infertility, was to prevent species in nature getting mixed up. Both of these doctrines we are now inclined to look upon with considerable scepticism—the accurately-careful experiments of Kölreuter, Gärtner, Darwin, and others, having demonstrated that these views were by no means founded on an accurate or extensive basis of observation. It is true, indeed, that first crosses between distinct species and between hybrids are very generally sterile, but, as will be shown, by no means invariably so. Hitherto botanists have confounded two classes of facts widely different—viz., hybridity of intercrosses of species, and of the hybrids produced from them. In the first the organs of reproduction are *perfectly*, in the second *imperfectly*, developed.

Degrees of Sterility.—The researches of Kölreuter and Gärtner show that there is a "high generality of some degree of sterility" among hybrids. Still they think that a certain degree of sterility between two distinct species is a certain law of nature. They show, however, that fertility or non-fertility is by no means a test of distinctness of species: for two plants, like the red and blue pimpernel (*Anagallis arvensis* and *cœrulea*), almost universally believed to be only varieties, are absolutely sterile when crossed; and, again, very distinct species are fertile under similar circumstances. However, so difficult is it sometimes to know whether a hybrid has decreased in fertility, that Kölreuter and Gärtner, from exactly the same experiments in one case, arrive at diametrically opposite conclusions. In many cases so little is the difference that, in order to see whether the fertility has decreased in the hybrid, Gärtner was obliged to count the seeds in both forms, concluding that if the seeds were fewer in the hybrid than in the pure species, the decreased number showed sterility commencing. Dean Herbert, on the contrary, is emphatic in declaring that some hybrids are as fertile as the pure parent species. In his careful experiments, every ovule of *Crinum Capense*, fertilised by *C. revolutum*, produced a plant—a result which never occurred when the plant was naturally fecundated. Some species of *Lobelia* are more easily fertilised by the pollen of another species than by their own pollen; and all the individuals of all the species of *Hippeastrum* are in the same predicament—viz., producing seed to the pollen of another species, though not to its own—though this pollen was perfectly good, as is proved by its producing seed if applied to the stigma of another species. So that there are individual plants, and all the individuals of certain species, which can actually be hybridised more readily than they can be self-fertilised. It is just possible, however, that the plants on which Mr Herbert tried his experiments were in an unnatural state, as frequently happens with plants in a state of domestication in hothouses.

It is, however, remarkable that a hybrid from *Calceolaria integrifolia* and *C. plantaginea*, species widely dissimilar in habit, reproduced itself "as perfectly as if it had been a natural species from the mountains of Chili." Hybrids between many distinct species of *Rhododendron—e.g.*, *R. Ponticum* and *R. Catawbiense*—as is well known to horticulturists, seed freely. Mr Anderson-Henry has found that *Veronica Andersonii*, a hybrid between *V. Lindleyana* (mater) and *V. speciosa* (pater), yielded seeds, perhaps in greater abundance than, and of equal fertility with, those of either of its parents. The same was true of a cross between *V. elliptica*, Hook., of the Falkland Island, and *V. speciosa* of New Zealand; though in another cross between *V. saxatilis* and *V. fructiculosa*, the seeds of the second generation produced no seeds which vegetated; and in other cases—a cross between two rhododendrons (*R. Dalhousiæ* and *Nuttallii*)—the seeds, though produced in great abundance, and germinating freely, died in every instance after they came above ground.[1] Had hybrids gone on decreasing generation after generation, as Gärtner asserts, nurserymen would surely have known it. Nurserymen, on the contrary, raise large beds of the same hybrid, and these, growing closely together, are often fertilised by each other's pollen naturally, and by the efficacy of insects; so that what occasioned Gärtner's observation—namely, sterility produced by the evil effects of interbreeding—is prevented. It may be remarked that with annuals it is different, perfectly fertile hybrids being almost unknown. Most curiously, Mr Anderson-Henry found that it was almost universally true that an American species crossed much more easily with an Asiatic than with another American species, or *vice versâ*, or especially with European species; and he also found it much easier to intercross plants of the southern hemisphere—however remote their homes might be. For instance, Australian and New Zealand species crossed more "kindly" with their allies of South America than with European

---

[1] Trans. Bot. Soc. Edin., ix. 112.

or kindred species in the northern hemisphere. American species have also a greater aversion to cross with European than with Asiatic species, and Asiatic species have no less aversion to intermix with European kinds. The whole question of how far hybrids between species and other hybrids are fertile, may be summed up as follows: "*Some degree of sterility, both in first crosses and in hybrids, is an extremely general result; but it cannot, in the present state of our knowledge, be considered as absolutely universal.*"

Laws governing the Sterility of First Crosses and of Hybrids.—(1.) Both first intercrosses and hybrids vary in their degree of fertility, from zero upwards to perfect fertility, as has been shown in the foregoing paragraphs. Mr Darwin has remarked, that when the pollen from a plant of one family is placed on the stigma of a plant of a distinct family, it exerts no more influence than so much inorganic dust; and from this absolute zero of fertility, the pollen of different species of the same genus, applied to the stigma of some one species, yields a perfect gradation in the number of seeds produced up to nearly complete, or even quite complete, fertility—in some abnormal cases, even to an excess of fertility beyond that which the plant's own pollen will produce. The same law holds good with hybrids themselves. The most incipient sign of the hybrid being slightly fertile with another, is when its flowers begin to fade rather earlier than they would if unfertilised; for early withering of the flower is well known to be a sign of incipient fertilisation.

(2.) Hybrids from two species which are difficult to cross, and which rarely produce any offspring, are generally very sterile. This law is, however, by no means strict in its parallelism—*i.e.*, between the difficulty of making a first cross and the sterility of the hybrids thus produced. For there are instances in which it is very easy to make a cross between two pure species, and yet the hybrids produced from this union in great numbers are unusually sterile; and the contrary is true—often, as in *Dianthus*, within the limits of the same genus.

(3.) Fertility of first crosses and of hybrids is more easily affected by unfavourable circumstances than is the fertility of pure species. Fertility is likewise innately variable; for it is not always the same when the same two species are crossed, but depends on the individuals which happen to be chosen for the experiment. The same is true as regards hybrids; for often the fertility will be found to differ greatly in the several individuals raised from seed out of the same capsule, and exposed to the same conditions of life.

(4.) When a biologist speaks of "systematic affinity," he means the resemblance between species in structure, and more especially the resemblance in those parts which, like the stigma, stamens, ovary, &c., are of physiological importance, and do not differ greatly in closely-allied species. Now, another law brought out by the researches of Kölreuter and Gärtner,[1] to whom we are almost entirely indebted for all these laws, is, that species most easily crossed have generally the closest systematic affinity—*e.g.*, species from different families can *never* be crossed, while those of one genus can often, indeed almost invariably, be.

This, however, is also not a strict law—for a multitude of closely-allied species will not unite at all, or with difficulty; and, on the other hand, very distinct species unite with the greatest facility. In the same family there may be a genus like *Dianthus* (the pinks), many of the species of which may be crossed; and another, like *Silene* (the campions), in which not one can be crossed with the other. Even within the limits of the same genus there are differences. Many species of *Nicotiana* (tobacco) have been more largely crossed than the species of any other genus; but Gärtner found that *N. acuminata* would not fertilise or be fertilised by no less than eight other species of *Nicotiana*. These facts open up to the botanist a wide and important field of investigation. For instance, at this present moment we cannot say what amount of difference or likeness is conducive or otherwise to crossing; for plants widely different in general structure, pollen, fruit, cotyledons, &c., can be crossed, and difference of habit presents in some cases no obstacles. Annuals can be crossed with perennials, deciduous with evergreen plants; while the most extreme differences in situation, climate, and generally habitat, present in some instances not the slightest difficulty in the way of their intercrossing; and, as has been shown, others, though closely allied, would not intercross.

(5.) By a "reciprocal cross," Mr Darwin means a case, for instance—taking a familiar example from the animal kingdom—of a stallion-horse being first crossed with a female ass, and then a male ass with a mare. These two species may then be said to have been reciprocally crossed. He shows that there is often the widest possible difference in the facility of making reciprocal crosses. These cases are important, as showing that the capacity in any two species to cross is widely independent of systematic and other affinity—in fact, of everything, except some difference in their reproductive organs. For instance, Kölreuter shows that *Mirabilis jalapa* can be easily fertilised by the pollen of *M. longiflora*, and the hybrids resulting therefrom are sufficiently fertile; but he tried in vain, more than two hundred times during the eight years following the foregoing experiment, to fertilise reciprocally *M. longiflora* with the pollen of *M. jalapa*. Thuret has ob-

---

[1] Beiträge zur Kenntniss der Befruchtung (1844).

served the same fact with certain Algæ. Gärtner has found that this difference of facility in making reciprocal crosses is extremely common in a lesser degree. Even between plants like *Matthiola annua* and *M. glabra*, so closely allied as often to be ranked as varieties, this is found. It is also a remarkable fact that hybrids raised from reciprocal crosses—though, of course, compounded of the very same two species, the one species having first been used as the father and then as the mother—though they rarely differ in external characters, yet generally differ in fertility in a small, and occasionally in a high degree.[1]

(6.) Some species have a remarkable power of impressing their likeness on their hybrid offspring; other species of the same genus have an equally remarkable power of crossing with other species; but these powers do not at all necessarily go together. There are certain hybrids which, instead of having, as is usual, an intermediate character between their two parents, always closely resemble one of them; and such hybrids, though externally so like one of their pure parent species, are, with rare exceptions, extremely sterile. Again, among hybrids which are usually intermediate in structure between their parents, exceptional and abnormal individuals sometimes are born which closely resemble one of their pure parents, and their hybrids are almost always utterly sterile, even when the other hybrids raised from seed from the same capsule have a considerable degree of fertility. These facts show how completely fertility in the hybrid is independent of its external resemblance to either pure parent.[2]

Uses of Hybridism.—Darwin, to whom in this, as in almost every other department of philosophical botany, we lie under such a deep debt of gratitude for his careful observations and thoughtful generalisation (apart from all questions affecting the theory more familiarly associated with his name), after considering the above rules, derived from Gärtner, has arrived at the following conclusion regarding the use of hybridism in the economy of nature. His idea is—and we can see no other conclusion which can be arrived at after studying the facts—that sterility is not, as was once supposed, a provision of nature to prevent species from being confounded in nature. For if so, why should the sterility be so different in degree when various species are crossed, all of which we must suppose it would be equally important to keep from blending together? Why should, he asks, the sterility be innately variable

---

[1] Origin of Species, 4th ed., p. 306. That the products of reciprocal crosses are perfectly alike, and that it is no matter which is the male and which the female parent—as taught by Max Wichura—Mr Berkley, and still more so Mr Anderson-Henry, in the most positive terms dissent from. Mr Anderson-Henry has known many instances of hybrids taking sometimes to one side and sometimes to another, but most frequently to that of the mother.

[2] Ibid., p. 306.

in individuals of the same species? Why should some species cross with facility, and yet produce very sterile hybrids, and other species cross with extreme difficulty, and yet produce fairly fertile hybrids? Why should there often be so great a difference in the result of a reciprocal cross between the same two species? Why, again, it may be even asked, has the production of hybrids been permitted at all, if it was so absolutely necessary to keep species from being blended together? "To grant to species the special power of producing hybrids, and then to stop their further propagation by different degrees of sterility, not strictly related to the facility of the first union between their parents," the illustrious naturalist whom we have quoted pertinently remarks, "seems to be a strange arrangement."

On the contrary, he thinks that the foregoing rules and facts "appear to clearly indicate that the sterility, both of first crosses and of hybrids, is simply incidental, or dependent on unknown differences in their reproductive systems—the differences being of so peculiar and limited a nature that, in reciprocal crosses between two species, the male sexual element of the one will often freely act on the female sexual element of the other, but not in a reversed direction." Mr Darwin illustrates his meaning by a reference to the laws of grafting. As the capacity of one plant to be budded or grafted on another is of so little importance to it in a state of nature, no one will suppose that this capacity is a *specially* endowed quality, but will admit that it is incidental in differences in the laws of growth of the two plants, in the rate of growth, hardness of their wood, in the period of the flow or the nature of the sap, &c., though in a multitude of cases we can assign no reason whatever. Great diversity in the size or nature of plants does not always prevent the two grafting together. As in hybridisation, so with grafting, the capacity is limited by systematic affinity, for no one has been able to graft together trees belonging to quite distinct families; and, on the other hand, closely-allied species, and varieties of the same species, can usually, but not invariably, be grafted with ease. But, as in hybridisation, this capacity is not absolutely governed by systematic affinity. For instance, the pear can be grafted more readily on the quince, which belongs to a different genus, than on the apple, which belongs to its own genus (Pyrus). Even different varieties of the pear take with different degrees of facility on the quince; so do different varieties of the apricot and peach on certain varieties of the plum.[1] Gärtner found that there was sometimes an innate difference in *individuals* of the same species in crossing; so Sagaret believes to be the case in grafting. As in reciprocal crosses, the facility of effecting a union is often very far from equal, so it is sometimes in grafting.

---

[1] Origin of Species, p. 309.

The common gooseberry, for instance, cannot be grafted on the currant; whereas the currant will take, though with difficulty, on the gooseberry. Something additionally analogous occurs in grafting to what occurs in hybrids, which, we have seen, have their reproductive organs in an imperfect condition. These hybrids being crossed is a different case from the difficulty of uniting two pure species. For instance, Thouin found that three species of *Robinia*, which seeded freely on their own roots, and could without much difficulty be grafted on another species, when thus grafted were rendered barren. On the other hand, certain species of *Sorbus*, when grafted on other species, yielded twice as much fruit as when on their own roots. The student will remember the analogous cases of *Hippeastrum*, *Passiflora*, &c., which seeded more freely when fertilised with the pollen of other species than when fertilised with their own.

We thus see that the "use" of hybridism is no more to prevent species getting blended in nature, than the "use" of grafting is to prevent the forest-trees inarching with each other.[1]

Origin and Causes of the Sterility of First Crosses and Hybrids.—We now come to consider a much more obscure question—one, no doubt, full of the deepest interest, but at the same time leading us further into the realms of fancy and speculation than we can go in this place. Mr Darwin concludes that the sterility of first crosses and hybrids is due simply to incidental or unknown differences in the reproductive systems of the parent species. Some curious observations have been made on this point. Sometimes there is a physical impossibility in the male element reaching the ovule, as in long-pistilled plants like the evening primrose (*Ænothera*), where it would be simply impossible for the pollen-tube to reach down from the surface of the stigma to the ovules.

Again, it has been observed, if the pollen of one species is spread on the stigma of a distantly-allied species, though the pollen-tubes protrude, they do not penetrate the stigmatic surface. In another case, the male element may reach the female element, and, as in some of Thuret's experiments on Algæ, have no effect.[2] Of this there can be no more explanation offered than why certain trees cannot be grafted on others.

Lastly, an embryo may be developed and perish at an early period. This has been known to be the case in animals and in plants also. At least hybrids raised from distinct species are often weak and sickly, and die early, as Max Wichura's experiments with willows have demonstrated. Plants, as well as animals, when in confinement, have their sexual organs much deranged,

---

[1] Origin of Species, p. 309, 310.

[2] See also Philbert, Observations sur l'hybridation dans les mousses, Ann. des Sc. Nat. Bot., xvii. (1873) 225-240.

and to this is due many of the "sports" and other varieties produced by cultivation, so well known to the horticulturist. In addition, when, as in hybrids, two constitutions are mingled together, there is naturally much disturbance. Max Wichura considers that the sterility of hybrids, when and in whatsoever degree it occurs, is owing to this. As we will hereafter see, the illegitimate offspring of dimorphic and trimorphic plants being similarly affected makes this view rather doubtful, though adopted by some theorists and experimentalists.

Difficulties in understanding Hybridity.—There are many points in the present state of our knowledge of this subject which require further elucidation, or the nature of which, though the facts are known, we cannot clearly understand. For example, why should there be unequal fertility in hybrids produced from reciprocal crosses? Why should there be increased sterility in those hybrids which occasionally and exceptionally resemble closely either pure parent? And finally, to go to the root, though by no means to exhaust the difficulties, of the subject, no explanation founded on well-ascertained facts can be given why an organism, when placed under unnatural conditions, is rendered sterile.

The good Effects of Intercrossing.—As in the animal, so in the vegetable kingdom, close interbreeding with the nearest relatives always induces weakness and sterility in the offspring. Accordingly, this crossing described in the foregoing pages is productive of good to the offspring and to the race generally. Even with hermaphrodite species a certain amount of intercrossing is indispensable; for, from the agency which insects must play in the fertilisation of certain plants, no other conclusion is possible (*vide* p. 437 for a discussion of this subject). It may almost be taken as a law of nature, that slight changes in the condition of life benefit all organic beings; and that, while slight crosses between the male and the female of closely-allied species or varieties add to the vigour and fertility of the offspring, on the contrary, crosses between more distantly related species produce hybrids which are in general sterile in a greater or less degree.

It is certainly a singular fact that the mere external appearance of two forms—no matter how dissimilar—in no way regulates whether they will cross or not. It is dependent on something in the constitution of the plants which we do not understand. Domestic varieties of plants like the cabbage, turnip, &c., are perfectly fertile; and it seems probable that a long course of domestication serves to eliminate the sterility produced in the first crosses. It has, however, been shown, by the experiments of Gärtner on maize, and Girou de Buzareingues on gourds, that sometimes acknowledged varieties are sterile. Gärtner, who strongly inclines to the belief that species which are infertile when crossed are distinct species, remarks that from long experiments he found that the yellow and white varieties of *Verbascum*, when intercrossed, produced less seed than when fertilised with their own pollen; and that when crossed by distinct species they produced more seed—if the species they were crossed with was a variety of the same colour—than with another coloured variety. Kölreuter made somewhat similar experiments with tobacco.

We are as yet profoundly ignorant of the cause of all this, but we may safely conclude that it is owing to some unknown power impressed on the reproductive organs.[1]

Fertility of Varieties when crossed, and of their mongrel Offspring.—Between the so-called hybrid offspring of species and the so-called mongrel offspring of varieties there are few and unimportant differences; and, on the other hand, they agree in many important respects. The most important distinction is, that mongrels are more variable than hybrids; but hybrids from species which have been long cultivated are often very variable in the first generation. Hybrids, also, between very closely allied species, are more variable than those between very distant species—thus showing, according to Darwin, that variability graduates away. When mongrels and the more fertile hybrids are propagated for several generations, an extreme amount of variability in their offspring is notorious. The greater variability of mongrels may be due to the fact that they are generally the offspring of cultivated species more subject to variability, as in them there has been more recent variability.. There is, however, a very slight degree of variability in hybrids from the first cross, or in the first generation; and when this is contrasted with their extreme variability in the succeeding generation, the fact is curious and worthy of note,—Mr Darwin considering that this bears on and corroborates the view which he has taken on the cause of ordinary variability—viz., that it is due to the reproductive system being eminently sensitive to any change in the conditions of life, being thus often rendered either impotent, or at least incapable of its proper function of producing offspring identical with the parent form.[2]

---

[1] Since the publication of Darwin's great work—parvus *liber*, magnum *opus*—there have been published many observations on hybridism. The student will, however, find a synopsis in the last (6th, 1872) edition of the 'Origin of Species,' and in Mr Darwin's papers in the Journ. Linn. Soc., vi. 71, 151, vii. 69, viii. 169; and in Mr Anderson-Henry's sketch of the results of a quarter of a century's labours, in his address on "Pure Hybridisation" (Trans. Bot. Soc. Edin., ix. 206-231, and 101-115; and Journ. Roy. Hort. Soc., 1872). With the exception always of Mr Darwin's researches, it is perhaps the most valuable paper in the English language on the subject; and the student of hybridism cannot do better than make himself master of it, our space not admitting of more than mentioning it.

[2] Origin of Species, p. 332.

Gärtner considers that mongrels are more liable than hybrids to revert to either parent form. Max Wichura, on the other hand, doubts whether hybrids ever revert to their parent form ; and he experimented on the cultivated species of willows : while Naudin, from experiments on *cultivated* plants, asserts quite the contrary. On the other hand, the degrees and kinds of resemblances in mongrels and in hybrids produced from nearly-related species follow, according to Gärtner, the same laws. Both hybrids and mongrels can be reduced to either pure parent form by repeated crosses in successive generations (Darwin). Finally, we may mention that the experience of Esprit Fabre, Godron, Naudin, Lecoq, and others, shows that while in many cases hybrids are incapable of propagating, in other cases they are. Fabre, for instance, shows that *Ægilops tricitoïdes*, Req., is a hybrid of wheat and of *Æ. ovata*, or *Æ. triaristata.* Godron, Planchon, and Groenland found that after fecundating *Ægilops* with the pollen of different varieties of wheat, they could obtain well-characterised hybrids, which produced fertile pollen and seeds. Naudin, after experimenting on the genera *Primula*, *Datura*, *Nicotiana*, *Petunia*, *Linaria*, *Luffa*, and *Cucumis*, obtained forty hybrids, ten only of which were entirely sterile. Hybrids of the genus *Nyctago* especially showed a remarkable fixity.

DIMORPHISM AND TRIMORPHISM.

In several plants belonging to different orders two forms are found, the one form having long stamens and short pistils, the other a long pistil and short stamens, and with different-sized pollen-grains, but differing in no other appreciable way. These are called *Dimorphic* plants. In *Trimorphic* plants, again, there are three forms, differing only in the length of their pistil and stamens, in the size and colour of the pollen-grains, and in some other points in reference to their reproductive organs—not, however, of specific difference. "As in each of these forms there are two sets of stamens, there are altogether six sets of stamens and three kinds of pistils ; and these organs are so proportioned in length to each other, that in any two of the forms, half the stamens in each stand on a level with the stigma of the third form."[1] It has been shown, that in order to obtain full fertility with these plants it is necessary that the stigma of one form should be fertilised by pollen taken from the stamens of corresponding height in the other form. "So that with dimorphic species two unions, which may be called 'legitimate,'[2] are fully fertile ; and two,

---

[1] Origin of Species, p. 320; Journ. Linn. Soc., vol. vi. (1862).

[2] Or *heteromorphic.*

which may be called 'illegitimate,'[1] are more or less infertile. With trimorphic species, six unions are legitimate or fully fertile, and twelve are illegitimate or more or less infertile."

Infertility in illegitimate unions—*i.e.*, by pollen taken from the anther of the stamen not corresponding in height with the pistil—differs in all degrees from fertility up to absolute sterility, just as happens in crossing distinct species, and as in that it depends much on the conditions of life being more or less favourable. One of the most curious observations in hybridism is, that if the pollen of a distinct species is placed on the stigma, and then after a considerable time the pollen of the species itself, it is so prepotent as to extinguish the effect of the other, and exert its influence. The same effect is seen in the fertilisation of dimorphic and trimorphic plants—the two forms, though *specifically* the same, behaving in this respect exactly as if they had been distinct species.

The law which we find in making reciprocal crosses between the same two species—viz., that there is often a great difference in the result — holds true also with dimorphic and trimorphic forms; for a long-styled cowslip, as shown by Darwin, yields more seed when fertilised by the long-styled form, and less seed when fertilised by its own form, than does a long-styled cowslip in the two corresponding methods. It is thus seen that there is something analogous to hybridism in this; for in all respects these forms, when intercrossed, behave as if they were separate species. Seedlings raised from "illegitimate" unions are not fully fertile; and in many ways, again, correspond to hybrids in their behaviour with other illegitimate plants. It is therefore no exaggeration to say that these are really hybrids—" produced, however, within the limits of the same species by improper union of certain forms, whilst ordinary hybrids are produced from an improper union between so-called species."

Darwin illustrates this generalisation by supposing that a botanist found two well-marked varieties (and such occur) of the long-styled form of the trimorphic—*Lythrum salicaria* (a species of Loosestrife)—and that he determined to try by crossing whether they were specifically distinct. He would find that they yielded about one-fifth of the proper number of seeds, and that they behaved in all other respects as if they had been distinct species. " But to make the case sure, he would raise plants from his supposed hybridised seed, and he would find that the seedlings were miserably dwarfed, and utterly sterile, and that they behaved in all other respects like ordinary hybrids. He might then maintain that he had actually proved, in accordance with the common view, that his two varieties were as good and as distinct species as any in the world; but he would be completely mistaken."

---

[1] Or *homomorphic.*

Further to illustrate this subject, we may give the results of the experiments of Hildebrand[1] on a trimorphic *Oxalis* (*O. Valdiviana* and *O. Regnelli*): 28 flowers with long styles, fecundated with pollen from flowers with long stamens, produced 28 capsules, each containing on an average 11.9 fertile seeds; 23 flowers with long styles, fecundated with pollen from median stamens, produced 2 capsules, which together only furnished a single seed; 14 flowers with long styles, fecundated with pollen from short stamens, produced no capsules at all; 38 flowers with median styles, fecundated with pollen from median stamens, produced 38 capsules, containing on an average 11.3 seeds.

Thus we see (1.) that infertility is no sign of distinct species, in any sense in which we can use the term. The red and blue pimpernels are not altogether fertile, hence they have been ranked as varieties. But this is simply reasoning in a circle. The colour of the flower, it may, however, be remarked, though in no way changing the structure, is attended with some constitutional derangements, rendering intercrossing difficult.[2]

(2.) That there "must be some unknown law or bond connecting infertility, both of legitimate unions and of first crosses, with the infertility of the legitimate and hybrid offspring."

(3.) We find that two or three forms of the same species may exist, and differ in no respect save in certain characters in their reproductive organs,—viz., in the relative length of the stamen and pistils; size, form, and colour of the pollen-grain; in the structure of the stigma, and in the size of the seed,—and yet have nearly all the characters of hybrids.

We have entered somewhat more fully on this subject than is usually done in elementary works, not only because the subject is of great interest and of the deepest importance, but because, though only recently called attention to, it is exerting the gravest interest among all philosophical botanists who rightly appreciate the bearing and dignity of their science, and will continually increase in importance. For our knowledge of it we are mainly indebted to the researches of Charles Darwin,[3] though it was dimly foreshadowed by Dillenius;[4] and the subsequent researches of Hugo von Mohl,[5] Fr. Hildebrand,[6] and A. S. Œrsted,[7] Oliver,[8] Delpino,

---

[1] Bot. Zeitung, 1871, Nos. 26 and 27.

[2] Bentham's Address to the Linnean Society, 1860, p. 91.

[3] Journ. Linn. Soc. Bot., vi. (1862) 77, vii. (1864) 69, viii. (1864) 169, x. (1868) 393, 437.

[4] Hortus Elthamiensis, 1732.

[5] Einige Betrachtungen über dimorphe Blüthen; Bot. Zeit., 1863, p. 309.

[6] Die Geschlechter-Vertheilung bei den Pflanzen, 1867.

[7] Et Bidrag til Kundskab om dimorfe og dichogame Blomster; Vidensk. Meddel. fra den Naturhistoriske Forening i Kjöbenhavn, 1869, p. 68.

[8] Natural History Review, 1862; see also, Parish on Dimorphism of *Cymbidium tigrinum*, Journ. Linn. Soc. Bot., x. 505.

and A. W. Bennett, have contributed to the literature of the subject.

Mr Darwin's observations were made chiefly on Primulas. Having covered up a pot of long-styled and another of short-styled primulas, the most part of them flowered, but did not produce seeds. Hence he considered that the agency of insects was necessary for their fecundation; but as he never saw an insect visit the plant during the day, he considered that probably night-moths might visit them for the sake of their honey. He tried to imitate the action of insects in searching for the honey of the flowers, and, as we have seen, the results were of great interest. If we introduce into the corolla of a short-styled cowslip the proboscis of a bee, the pollen of the anthers, situated at the entrance of the tube, adheres around the base of the proboscis; and it will necessarily happen that when the insect visits subsequently a long-styled cowslip, the pollen so taken up will be scattered on the stigma of that plant. But in that new visit to the long-styled cowslip, the proboscis, in descending to the bottom of the corolla, will find the pollen of the anthers which lie at the bottom of the tube, and that pollen will attach itself to the summit of the proboscis; and if the insect should visit a third flower which is short-styled, the tip of the proboscis will touch the stigma situated at the base of the corolla, and there deposit the pollen.

Furthermore, it is necessary to admit as probable that in the second visit mentioned above—to the long-styled flower—the insect, in retracting its proboscis, would leave upon the stigma a part of the pollen taken from the anthers situated below; and thus the flower would become self-fecundated. On the other hand, it is almost certain that the insect, in stretching its proboscis into the short-styled corolla, will have brushed against the anthers inserted at the top of the tube, and thus caused a certain quantity, more or less, of the pollen to be shed on the stigma of its own flower.

Finally, the corolla of the cowslip contains, in abundance, minute insects belonging to the genus *Thrips*, of the order *Hemiptera*, which run about the flower in every part, transporting the pollen of the anthers to the stigma. Thus, again, the plant will be, by another agency, self-fecundated. Hence, in the fecundation of dimorphic species, there are four operations possible,—viz., 1st, fecundation of the long-styled flower by itself; 2d, of the short-styled flower by itself; 3d, of the short-styled flower by the long-styled; and, 4th, of the long-styled by the short-styled flower.

Darwin has further remarked, that while these dimorphic and trimorphic plants cannot fecundate themselves, this may be partially done by the agency of currents of air, if the pollen is dry; for if the corolla is without colour, no honey is secreted. If, on the contrary, the corolla is brilliant, honey is secreted, and insects most effectually discharge the office of carrying the pollen from one flower to another.

Among American plants, dimorphism can be seen in the common *Houstonia* and the Partridge-berry of the northern woods, while trimorphism is seen in *Nesæa verticillata* (a species of Loosestrife), &c.

The use of Dimorphism and Trimorphism.—To prevent the pollen from the anthers of a flower acting on the stigma of the same flower, and thus, by too close inbreeding, causing the plant to lose its vigour. The gain in this case has been obtained at the expense of all the plants of the same form being rendered more or less sterile with the same form, both in first cross and in their offspring. Hooibrenk and Kœrnicke[1] have even attempted to carry this into practical agriculture in Belgium and Germany, by drawing a rope across the full-flowering ears of a field of corn, and thus causing the plants to be fertilised by the pollen of different individuals, by the rope slightly brushing the ears of grain. It appears to have been useful in some cases in increasing the yield of certain crops.

DICHOGAMY.[2]

We have already remarked that though, for the sake of convenience, when speaking for the first time of the fertilisation of the ovule by the pollen, we considered the *typical* method by which this was accomplished was simply—in the greater body of plants which had both sexes on one flower (hermaphrodites)—by the pollen of the anther falling on the stigma of its own pistil, ready, simultaneously with the anther, to accomplish

---

[1] Gartenflora, 1866, s. 29.

[2] Sprengel first used this term (dichogamia) in the sense now used in contradistinction with what he called "Homogamy" (homogamia)—*i.e.*, "when both parts of a generation are formed in a hermaphrodite flower exactly at the same period." This seems identical with what Hildebrand proposed the term "non-dichogamy" for—an inconvenient expression, for which Alfred Bennett has proposed to substitute "Synacmy." "Protandry" and "Protogyny"—expressions first used by Hildebrand, and corresponding to Sprengel's "Dichogamia androgyna" and "Dichogamia gynandria"—Mr Bennet has proposed ('Nature,' 1870, p. 482) to express under the general term of "Heteracmy." Both these words are good; but still Sprengel's term *Homogamy*, which is faultless in expression, has a prior claim over Bennett's *Synacmy*. In this text-book I have used Sprengel's term *Homogamy* in the same sense as he did (having, indeed, resolved to do so before I was aware of Sprengel's prior use of it); while all other modes of fertilisation—dichogamy, dimorphism, trimorphism, &c.—I have comprehended under the term Heterogamy.

fertilisation; we furthermore showed certain mechanical contrivances by which this was accomplished. In monœcious and diœcious plants this fertilisation could, of course, not be so accomplished unless accidentally; and to accomplish this the agency of insects was necessary. However, as the student has proceeded with the study of fecundation, he will have found that the time-honoured idea we have mentioned admitted of many exceptions, and that, indeed, the most elaborate contrivances exist to absolutely prevent the pollen of each flower from acting on the stigma of that flower.

In orchids and other plants we will see how this is accomplished by many curious mechanical contrivances. Thus, we have already seen that hybridity is of the most common occurrence: and in our last paragraph we find the same end gained by dimorphic and trimorphic flowers, in which the pollen of each flower, and consequently of the flowers of the same form, has been rendered more or less impotent on their own stigmas; so that its action is easily and wholly obliterated by pollen habitually brought from other individuals and forms of the same species.[1]

Finally, nature, as if lavish of her powers to accomplish the same end by the most diverse means, has made another provision for the same purpose—one long known to botanists, though until recently its import and bearings were not sufficiently appreciated, or forgotten. As early as 1793, Karl Konrad Sprengel—then Rector at Spandau—in his remarkable work, 'Das Entdeckte Geheimniss der Natur in Bau und in der Befruchtung der Blumen' (The Secrets of Nature in the Structure and Fecundation of Flowers), described certain plants in which the anthers and the stigma are never ripe at the same time, so that these plants can never fertilise themselves. These he called *Dichogamous* plants. Those in which the stamens were ready to discharge their pollen before the stigma was ready to receive it (*e.g.*, Foxglove, *Epilobium angustifolium*, *Ranunculus repens*, *Silene inflata*, *Geranium pratense*, *Campanula rotundifolia*, &c.) are called protrandrous; and those in which the stigma is ready to perform its functions before the anther is ready to discharge the pollen, *protogynous* (e. g., *Potentilla anserina*, *Erythræa Centaurea*, *Plantago*, &c.) These dichogamous plants are found in many orders—such as Malvaceæ, Geraniaceæ, Umbelliferæ, Scrophulariaceæ, Campanulaceæ, Lobeliaceæ, Gramineæ, all of the Compositæ (protrandrous, according to Hildebrand), Scitaminaceæ[2] (*Calathea grandiflora*, Lindl.), &c. A few familiar examples will suffice to explain it.

---

[1] Origin of Species, p. 325.

[2] Œrsted, Vidensk. Medd. fra den Nat. Hist. For. Kjöb., 1869, p. 73. For list of protrandrous and protogynous plants, see A. W. Bennett in Seemann's

In Leguminosæ and Labiatæ, all the species, with scarcely an exception, range themselves into the protrandrous, protogynous, or homogamous series, while in *Rosaceæ* and some others they are distributed over all three; and in some instances even closely-allied species of the same genus differ in this respect—as, for instance, *Potentilla* and *Ranunculus*. In those natural orders in which the flowers are furnished with two sets of stamens of different lengths, it is most usual for the longer ones to discharge their pollen at an earlier period than the shorter ones; and they have probably different functions to perform. Such plants are therefore both dimorphic and dichogamous. This is commonly the case with *Cruciferæ*, *Caryophyllaceæ*, *Geraniaceæ*, and *Onograceæ*, but not, apparently, with *Labiatæ* or *Scrophulariæ*. The same phenomenon is found in those orders where the numerous stamens are arranged in different whorls, as *Ranunculaceæ* and *Rosaceæ*.[1]

In *Lobelia fulgens* (another of these dichogamous plants) there is an elaborate and beautiful apparatus, by which all the numerous pollen-grains are swept out of the conjoined anthers of each flower before the stigma of that individual flower is ready to receive them. Now, Mr Darwin noticed that, in his garden at least, this *Lobelia* was never visited by insects; while another species growing close by, which was visited by bees, seeded freely. However, if the pollen from one flower was placed on the stigma of another, it raised abundance of seedlings from it. In many other cases the anther bursts before the stigma is ready for fertilisation, or the stigma is ready before the pollen of that flower is ready. In a word, these plants have, to all intents and purposes, separate sexes *physiologically*, though *anatomically* they are hermaphrodite. The same may be said of the dimorphic and trimorphic plants. All this would be strange and inexplicable except on the view of an occasional cross with a distinct individual being beneficial or indispensable to the life of the plant. In fact, in the berberry, a hermaphrodite plant, specially endowed, as we will see (Sect. IV.), with an apparatus for scattering the pollen over the stigma, so large is the capacity for intercrossing, that it is well known that if closely-allied forms or varieties are planted near each other, it is hardly possible to raise pure seedlings (Darwin). Darwin found that if several varieties of the cabbage, radish, onion, and of some other plants, be allowed to seed near each other, a large majority will turn out mongrels. Yet the pistil of each cabbage-flower is surrounded not only by its own six stamens, but by those of the many other flowers on the same plant; and the pollen of each flower

---

Journal of Botany, Oct. 1870 and Nov. 1871; also his Paper in Pop. Sc. Rev. October 1873; and "How Flowers are Fertilised," Manchester Sc. Lectures, Nov. 5, 1873.

[1] A. W. Bennett in 'Nature,' 1870, p. 482.

readily gets on its own stigma without insect agency—for in one of his experiments it was found that a plant carefully protected yielded its full number of pods. How, then, does it happen, he asks, that such a vast number (scarcely 78 out of 233 seedling cabbages grown by him were true to their kind) are mongrelised? "I suspect that it must arise from the pollen of a distinct *variety* having a prepotent effect over a flower's own pollen, and that this is part of the general law of good being derived from the intercrossing of distinct individuals of the same species. When distinct *species* are crossed, the case is the reverse; for a plant's own pollen is almost always prepotent over foreign pollen"—as we have already seen when discussing hybrids.

Campanula, Scrophularia, &c., are all protrandrous; but one of the most beautiful examples of protrandry is exhibited by *Clerodendron Thomsonæ,* Balf., a plant from the Old Calabar River in West Africa, but now very common in our conservatories. "Four stamens, with very long filaments and an equally long slender style, are rolled up together in the corolla bud. When this expands, the stamens straighten out nearly in the line of the tube of the corolla, and their anthers open; the style has bent so far forward as to point downwards; and the stigma is not yet ready for pollen, its own branches being united. So a butterfly in the act of drawing nectar from this flower will get the under side of its body dusted with pollen, but will not come near the reflexed or still immature style. But in a flower a day older the stamens are found to be coiled up (the opposite way from what they were in the bud), and turned down out of the way, bringing the anthers nearly where the stigma was the day before, while the style has come up to where the stamens were the day before; and its stigma, with branches outspread, is now ready for pollen—is just in position and condition for being dusted with the pollen which the butterfly has received from the anthers of an earlier blossom."

Let us now examine the "grass of Parnassus" (*Parnassia palustris*), a common plant of northern bogs and swampy heaths, and an excellent specimen of a protrandrous plant. Though known for long, it is only recently that its reproductive organs have been correctly described. Its affinities are doubtful, some botanists putting it among the *Hypericaceæ*, others among the *Droseraceæ;* a third party consider that its nearest allies are the *Saxifragaceæ;* while a fourth section have solved the question by constituting it an order by itself—viz., the *Parnassiaceæ.*[1] The flower is

---

[1] Cosson and St Pierre (Flore des environs de Paris, 1st ed.) consider it as the type of a special section of Droseraceæ; but they unite Droseraceæ and Pyrolaceæ into one order, called *Roridulaceæ*—so named from the genus *Roridula*, which by its characters forms a connecting link between the two

remarkable for its glandular petaloid scales, which have been supposed to be "modified polyadelphous stamens, united together at the base," and even as metamorphosed carpels[1]—both opinions being dubiously correct. The physiology of the phenomena of fecundation is, however, the most remarkable thing about it, and has been described by Vaucher, and more recently and more correctly by Mr A. W. Bennett.[2] The former author remarks, that when "the flower is fully open, the filaments, at first very short, suddenly lengthen and place the anthers on the top of the ovary; so that all the glandular globules, and especially the scale which bears them, and which is covered with little drops of honey, can dissolve the pollen with which they are sprinkled. This operation accomplished, the anther falls and disconnects itself, and the filament resumes its original place." Each of the anthers successively executes the same movement; but Bennett does not confirm Vaucher when he says that those which succeed each other are alternate and not contiguous—for the former author has frequently seen contiguous stamens to follow each other. "The anthers are extrorse and somewhat lateral—the pollen consequently cannot fall on the stigma, but falls on the nectaries, which are, as it were, smeared with it, and only the emanation from which can, I think, fertilise the stigmata. . . . The stigmata are entirely invisible while the anthers are discharging their pollen, and they only begin to display themselves, and expose their papillose tongues, at the moment when the emission is accomplished."[3]

The lengthening of the filaments to at least three or four times their original length is accomplished in an incredibly short space of time, and the adhesion to the ovary is so strong that they cannot be removed without breaking them; but once the pollen is discharged, they retire to a horizontal position between the petals, and the anther falls. Previous to the discharge of the pollen the anther contracts. Altogether, this is one of the most singular of all the arrangements in flowers to prevent cross-fertilisation. Not only is the back of the anther turned to the very apex of the pistil at the time of the ripening of the pollen, so as to close the approach to the ovary, but the stigmata (4-5 in number) are not developed until the anthers have discharged their pollen.

---

tribes *Drosereæ* and *Pyroleæ*. This arrangement has not been adopted by other botanists; and in the 2d ed. of their *Flore* the authors have dropped it, with the protest, however, that they still consider it good.

[1] Buchanau in Botanische Zeitung, xx. 307.

[2] Journ. Linn. Bot. Soc., xi. 25. See also Gris in Comptes rendus, Nov. 2, 1868.

[3] Hist. Physiologique des Plantes d'Europe, 324 (*fide* Bennett, l. c.); and Arthur Gris, "Sur le mouvement des Etamines dans le *Parnassia palustris*" (Mem. de la Soc. Nat. de Cherbourg, t. xvi., deux. ser. t. vi.), 1871-72.

The function of the nectaries is thus shown to be, not, as Vaucher supposed, for "the absorption of the pollen," in order to return it to its own stigmata, but to enable insects "to carry it away to other flowers in which the stigmata are already expanded."

Fertilisation by means of Insects.—From the frequent reference made to this agency while discussing the foregoing subjects, the student will have had little difficulty in arriving at the conclusion that the primary agents in effecting fertilisation in dimorphic, trimorphic, and dichogamic plants are insects. Linnæus was acquainted with dichogamous plants, but he supposed they were fertilised by the wind wafting the pollen to them. Kölreuter was the first to clearly state that insects served this purpose; but Sprengel, in his famous work already quoted, first clearly worked out the idea that insects assisted in fertilisation. Yet it is only within the last few years that the exact details of this curious subject have, to any extent, been elaborated. The odour and brilliant colours of flowers, or the instinct to seek for nectar, attracts beetles, butterflies, bees, moths, thripsidæ, ichneumons, various diptera, &c., to these flowers, and all are busy in assisting in this great work. To use the language of a famous American botanist, "Where 'free lunches' are provided, some advantage is generally expected from the treat." A knowledge of Transatlantic customs may be required to appreciate the humour of the illustration; but the results of insects thus feeding in flowers, and paying for their food by assisting in fertilisation, will be readily understood if the facts which follow are considered. In a word, to reach these supplies of nectar the insects are obliged to disturb the pollen-grains, which, being often viscid, attach themselves to the legs and heads of the insects, which thus unconsciously carry them off to impregnate the next "heteromorphic" flower they visit. Only those flowers which secrete a sweet juice are visited by insects, and chiefly those which are bright-coloured, or have bright-coloured spots—what Sprengel calls *maculæ indicantes*, as they indicate that a plant produces honey. Sprengel also declared—and I am not aware that eighty years' observation has disproved his assertion—that many insects are limited to one species of flower; while others that are not so confined visit many indiscriminately, but will, during a whole day, remain with the species on which they fixed in the morning, and will not visit another provided there be enough of the first species to provide them with work. Therefore, before dismissing this subject, let us briefly review the whole subject from this stand-point.[1] Among dichogamic plants protrandry is more common than protogyny. The important families of the

---

[1] See the work of Hildebrand, already quoted, for an admirable *précis* of this question; or a summary by M. Micheli, trans. by Mr Dallas in Ann. Nat. Hist., ix. 234, 4th ser.

Labiatæ, Scrophulariaceæ, Compositæ, and Campanulaceæ, belong to this category. Accordingly, the details of organisation are adapted especially for fertilisation by insects. For example, in all the Compositæ examined by Hildebrand,[1] the five stamens have the anthers soldered in a cylinder, which envelops the pistil; they open and allow the pollen to escape before the style has become elongated. The style bears, below the stigma, a certain number of rigid hairs, which retain the pollen-grains, and carry them forward with them in their ascending movement at the moment of the elongation of the style. The pollen thus carried up out of the cylinder of the anthers is collected by insects, and transported to flowers the stigma of which is already expanded. The same apparatus—though in a more variable form, as far as concerns the appendages destined to retain the pollen on the style—prevails in the *Campanulaceæ*, *Lobeliaceæ*, &c. "In the whole of the group of scrophulariaceous Labiatæ the axis of the flower is horizontal, and the stamens are approximated beneath the upper lip of the corolla. The insects, in passing, separate and jostle them, cause the pollen to fall from them, and then transport it to a more advanced flower. In certain genera the stamens stand alone in the way of the insects, which always seek the bottom of the flower, where the nectaries are. Later on they curve outwards, the style in its turn becomes elongated, and advances to take their place, and its recurved extremity caresses the body of the insect laden with pollen."[2]

In some of the Urticaceæ, the common nettle among others, several species of *Trophis*, *Batis*, &c., the filaments are bent down upon the disc until the pollen is ripe, when the slightest touch of a marauding insect causes them to spring, and scatter on every side a cloud of pollen. In the *Iris* "there is a stamen to each of the three stigmas, and close beside it. Behind each stamen, and partly overhanging it, is a petal-like body peculiar to the Iris: these three bodies, appearing like supernumerary petals, are divisions of the style, in a peculiar form notched at the end; and in the notch is the stigma, in the form of a thin plate. We notice that the stigma is higher than the anther; but that is only a part of the difficulty. The anther and the stigma face each other. The anther faces outwards, and discharges its pollen through two

---

[1] "Uber die Geschlechtsverhaltnisse bei den Compositen," Acta. Leop. Carol. Nat. Cur., vol. xxv. (1869); also in a separate form, p. 104. Hildebrand is, however, in error when he says that *all* the Compositæ are fertilised by the aid of insects, for it has been shown by Delpino that the sections *Ambrosiaceæ* and *Xanthiæ* are fertilised by the aid of the wind; and so important does he consider this, that he has given the name *Artemesiaceæ* (wormwood being one of the species) to all these *anemophilous Compositæ* (Studi sopra un lignaggio anemophile delle Composte, &c., Florence, 1871).

[2] "Ulteriori osservazioni sulla dicogamia nel regno vegetale," Atte della Soc. Ital. di Sci. Nat., vols. xi. and xii. (*teste* Micheli, l. c.)

long slits on the outer side only. The thin plate or shelf is stigma only on its upper or inner face, which is roughened and moistened in the usual way for receiving the pollen; the face turned towards the anther cannot receive the pollen at all." [1] There are hundreds of similar cases in which the pollen is placed close to the stigma, but can never, or at least only seldom or accidentally, reach it of itself. Insects alone can accomplish their fertilisation, as seen in the case of *Iris* quoted above. "A little nectar is produced in the bottom of the tube of the blossom. The only access to it is a narrow channel, leading down to the united bases of the six petals of the flower. Now the three inner of these are upright, with their lips curved inwards, shutting off all access in that quarter. But the three outer and larger divisions recurve, and afford a convenient landing-place directly before the stamen and the overarching stigma. Here the bee alights. To reach and suck out the nectar with his proboscis, will bring the head at least as low as the base of the anther. On raising his head to depart, he sweeps with it the whole length of the anther, and dusts it with the pollen now shedding. A little higher the shelf of the stigma is hit, but only the outer face of it, which is smooth, and does not take the pollen at all. Flying to the next blossom, the first thing which the pollen-powdered head of the bee strikes is the stigma, but this time on the upper face of the shelf, or real surface of the stigma, which takes some of the pollen brought into contact with it, and so is fertilised. Sinking lower, the head next brushes the anther downwards in entering for the nectar, then upwards in departing, and receives a fresh charge of pollen to be deposited upon the shelf of the stigma of the next blossom visited,—and so on."

In *Arethusa*, *Aristolochia*, *Kalmia*, &c., fertilisation requires equally the aid of insects. In the first genus no insects have yet been seen about the plant; but its structure shows that it must require their agency in fertilisation. In *Aristolochia* [2] (fig. 171) (birthwort), however, the process has been repeatedly observed. The long, contracted throat of the corolla is lined with hairs, and at the bottom expands into a chamber, where there is a broad sessile stigma, surrounded with the stamens, which are placed a little below it, and with their anthers turned away from the stigma, so that none of the pollen can fall on it. If an insect enters, the hairs prevent it making its exit; but as the flower advances, the hairs somewhat relax, and permit of the escape of the winged messenger laden with the pollen, which it has got covered with in its

---

[1] Gray, How Plants Behave (1872), p. 22.

[2] Insect fertilisation in *Aristolochia* was first accurately described by Sprengel. He considered that *Tipula pennicornis* was the insect which always effected this, at least in *A. Clematis*. *A. Sipho* (the pipe-vine, or Dutchman's pipe) of the United States also shows it well.

struggles at the bottom of the corolla to escape, and carry it to another plant, the stigma of which is ready to receive it. In *Kalmia*, another American genus, some species of which are common in our shrubberies, under the name of "American laurel," the anthers are contained in little pouches on the inside of the corolla, so that the ten stamens are bent all around the stigma in the form of springs. When a bee visits the flower to seek for honey, its proboscis lowers the stamen, which springs up with force, discharging, by the pores of the anther, pollen-grains, either on to the stigma or on to the insect, which flies to another flower with them, repeating the same process, and so aiding again and again in cross-fertilisation. Such is the account given by Professor Beal of Michigan, who states that if the flowers are covered with gauze, and insects thus prevented visiting them, no seeds set. It is thus probable that this, like many other plants, requires cross-fertilisation before impregnation can be effected.

What proves still more remarkably that self-fertilisation is of extremely rare occurrence in the vegetable kingdom is, that in certain families in which stamens and pistils get ripe simultaneously, and of necessity are spontaneously fecundated, the intervention of insects is equally required. For instance, in the order *Leguminosæ*[1] the stamens and pistils are united in the form of a sort of keel, so close together that it is impossible but that some of the pollen-grains at least will have fallen on the ripe stigma. Yet the fact is, that without the intervention of insects, carrying off the pollen from another plant, rarely is a single seed produced. The intrusion of the insect causes the staminal column to free itself from the place where it lies in the keel, and so cover the winged visitor with a cloud of pollen. Darwin showed that bees, in visiting the flowers of the scarlet kidney-bean, always alight on the left wing, and in so doing depress it. This immediately acts on the keel, which forces the pistil to protrude. On the pistil is situated a little tuft or brush of hairs, which, by the repeated movements of the keel, brushes the pollen from the anthers on to the stigmatic surface.[2] Hildebrand has shown[3] that in the

---

[1] "On the Fertilisation of a few Common Papilionaceous Flowers;" T. H. Farrer in 'Nature,' 1872, p. 478-498.

[2] Gardeners' Chronicle, Nov. 18, 1858.

[3] "Bestäubungsvorrichtungen bei den Fumariaceen," Pringsheim's Jahrbuch, Bd. vii. s. 423-471. On the same subject, with reference to the effect of insects in cross-fertilisation, see H. Müller, of Lippstadt, in Verhand. des naturhistoriche Ver. der preussischen Rheinlande u. Westphalens, 1869, Correspondenzblatt, s. 43 *et seq.;* and also to some extent Dr Buchanan White, in Journ. of Botany, Jan. 1873, p. 11-13. In a recent work (The Naturalist in Nicaragua, 1874), Mr Belt mentions that the scarlet-runners in his garden at Santo Domingo bloomed abundantly; but as none of the humble-bees of the country frequented the flowers, they never produced a single pod. The

Fumariaceæ, with the exception of *Hypecoum*, though the stamens and pistils are seemingly securely placed between two petals, out of reach of all ulterior influences, insects, to reach the store of nectar which is placed at the base of these organs, must pass between the petals, and so carry off pollen to fertilise another plant while searching for their food in a similar manner. Hence the showy "bleeding heart" (*Dielytra spectabilis*), which comes from Japan and China, rarely sets fruit in our gardens; while the wild species of *Corydalis* and fumitory do, *if not covered with gauze.* In some of the orders allied to the Fumariaceæ a similar arrangement prevails. For example, in *Canna* (Cannaceæ) the arrangements depend, according to Delpino, on the viscidity of the pollen and the bursting loose of the style; the pollen is first deposited on an expansion of the style, whence it is taken away by the insect, to be deposited on the stigma of the flower visited. The humble-bees, Darwin shows, are nearly indispensable to the fertilisation of *Viola tricolor* (heart's-ease), for other insects do not visit it. Bees are also necessary for the fertilisation of some kinds of clover. For instance, twenty heads of Dutch clover (*Trifolium repens*) yielded 2290 seeds; but twenty other heads, *protected from bees*, yielded, according to Darwin's observation, none. Again, he shows that while 100 heads of red clover (*T. pratense*) produced 2700 seeds, the same number of heads protected from the visits of insects were all sterile. Hence it may be logically inferred that, as no other insect visits the clover and heart's-ease, if the humble-bee was becoming scarce or extinct in England, the two plants named would either become very rare or perhaps altogether extinct.[1] It has been affirmed, by some objectors to Darwin's theory of the fertilisation of flowers by insects, that in *Salvia* the bees do not enter the corolla, but cut a hole on the outside in order to obtain the honey. This is not true, as bees have been seen repeatedly to enter the flower; and when they do cut a hole in the manner described, it is only when they are too large to get into the tube. Mr C. V. Riley of St Louis has only recently shown

---

flowers of the lofty climber, or "liana," *Marcgravia nepenthoïdes*, are disposed in a circle, hanging downwards like an inverted candelabrum. From the centre of the circle of flowers is suspended a number of pitcher-like nectaries, which, when the flowers expand in February and March, are filled with a sweetish fluid. This liquid attracts insects, and the insects numerous insectivorous birds. The flowers are so disposed, with the stamens hanging downwards, that the birds, to get at the pitchers, must brush against them, and thus convey the pollen from one plant to another. Many other interesting instances are given in the same book.

[1] See Darwin's discussion of this in Origin, &c., p. 83, 84, and p. 103-108. Field-mice destroy the nests and combs of the humble-bee; they are in their turn destroyed by cats,—and hence the existence of the species of clover named may be said to be dependent on the number of cats in a district!

that the American Yuccas are protrandrous, and that therefore the glutinous pollen must be conveyed to the stigma by some other agency. This agency is a little moth—*Pronuba Yuccasella*—which is the only insect which assists in this operation; and accordingly, in the Northern States and elsewhere, the Yuccas, though cultivated for their flowers, cannot seed, on account of the absence of the insect. The female insect only has the basal joint of the maxillary palpus wonderfully modified into a long prehensile-spined tentacle. With this tentacle she collects the pollen and thrusts it into the stigmatic tube, and after having thus fertilised the flower, she consigns a few eggs to the young fruit, the seeds of which her larvæ feed upon.[1] In *Duvernoia adhatodoides*, an acanthaceous plant of the Cape of Good Hope, Mrs Barber has shown that fertilisation is accomplished by a large hymenopterous insect of the genus *Xylocopa*, which insect fertilises no other plant.[2]

Fertilisation of Orchids.—*Anatomy of the Flower.*—We have already (p. 318) referred to the structure of the flowers of the orchids, and sufficiently remarkable they are in their anatomy; not less so is their physiology. Before, however, describing the function, it may be well to describe the general anatomy of the flowers, which we have left as most appropriate to this place. The flowers of this order are often most *bizarre* in form, simulating the appearance of various animals. To use the language of Mr Bateman: "Flies are seen in *Ophrys muscifera*, bees in *O. apifera*, drones in *O. fucifera*, spiders in *O. aranifera*. The columns of many of the Catasetums and other genera make excellent grasshoppers. Mosquitoes are borne by *Trichoceros antennifer*, or *Flor de Mosquito* of the Peruvians; dragon-flies by *Renanthera arachnites;* moths by *Phalænopsis amabalis.* Insect-like antennæ are also conspicuous in the flowers of *Restrepia antennifera.* The butterfly-plant of Trinidad is now the well-known *Oncidium Papilio.* Swans are found in the species of *Cycnoches;* doves in *Peristeria elata;* pelicans in *Cypripedium irapœanum*, which, from the great resemblance of its flowers to the bird of that name, is styled by the natives *Flor de pelicano.* The skins of the tiger and the leopard are rivalled by the petals of such plants as *Stanhopea tigrina*, *Bolbophyllum leopardinum*, &c. The *flos lyncea* of Hernandez (*Stanhopea Martiana*) is so called from its lynx-like eyes and teeth; *Dendrobium taurinum* has much of the bull about its face; and various *Cataseta*—*C. semiapterum* especially—grin like the ugliest monkey. *Aceras anthropophora*, the man-orchis, is a well-known plant. Even extinct animals do not always escape: a

---

[1] Paper read to Am. Assoc. for Adv. Science, Aug. 24, 1872. Reported in 'Nature,' 1872, p. 444.

[2] Journ. Linn. Soc. Bot., xi. (1871) 469-472.

geologist would instantly recognise the head of a *Dinotherium* in the flowers of *Masdevallia infracta*. *Pleurothallis ophiocephala* has a strong resemblance to a serpent's head, and *Pholidota imbricata* an equally strong resemblance to a rattlesnake's tail. Lizards occur in *Pleurothallis saurocephala* and *Epidendrum lacertinum*, and frogs in *Epidendrum raniferum*." The anatomy of the flower of an orchid is fully displayed in fig. 298, where will be found the dissection of one of the most common species which appear in early spring or summer. The perianth, as already mentioned (p. 318), is made up of six segments in two rows, these segments being generally coloured. The lowest (owing to the twisting of the ovary) differs in form from the other segments, is often spurred, and known as the *labellum*. It is frequently tripartite—*i. e.*, divided in three portions, distinguishable from each other. The lowest portion, when this is well marked, is known as the *hypochilum*, the middle *mesochilum*, and the upper the *epichilum*. The stamens and pistils are united into a single column, the *gynostemium* (p. 329). The stamens are three in number [1]—the outer two, and sometimes the central one, being abortive. The anthers are placed in a cavity at the apex of the column called the *clinandrium*. The pollen is rarely powdery, more frequently, as in the species figured (fig. 298, C and E), adhering in *pollinia* (p. 346). The stigma is an open space in front of the column, or gymnostemium. A small thickened process intervenes between the anther and the stigma, covering the latter over as with a roof, and acting as a floor to the former, and is called the *Rostellum;* in most orchids it secretes a viscid fluid. Finally, there is a spur-like nectary. The flower is thus so formed that, without extraneous aid, the pollinia could not escape from the anthers. But an insect (a moth, bee, &c.), while sucking the nectar from the flower, would detach the anther and expose the pollinia, which would attach themselves by their discs to its proboscis, and so enable these pollinia to be carried to another flower in the manner to be presently described.

Morphology of the Flowers of Orchids.—The exact morphology of the flowers of orchids is not yet settled, different authors taking different views in regard to the parts which are coalesced. Mr Darwin looks upon an orchid flower as consisting of five simple parts—namely, "three sepals and two petals" (not adopting the usual view of the monocotyledonous perianth); "and of two compounded parts—namely, the column and the labellum. The column is formed of three pistils, and generally of four stamens, all completely confluent. The labellum is formed of one pistil, and two petaloid stamens of the outer whorl, likewise completely con-

---

[1] Dr Masters has given (Veg. Terat., p. 383-387) a whole series of intermediate forms between the common orchid with one stamen only up to forms in which six are developed.

fluent. . . . This view of the nature of the labellum explains its large size, its frequently tripartite form, and especially its manner of coherence to the column, unlike that of the other petals." The six stamens or anthers, which ought to be represented in every orchid, are explained in this manner: "The three outer belonging to the outer whorl are always present, with the upper one generally fertile, and the two lower ones invariably petaloid and forming part of the labellum. The three stamens of the inner whorl are less plainly developed, especially the lower one, which, when it can be detected, serves only to strengthen the column, and in some rare cases, according to Brown, forms a separate projection or filament. The upper two anthers of this inner whorl are fertile in *Cypripedium*, and in other cases are represented either by membranous expansions or by minute auricles without spiral vessels. These auricles, however, are sometimes quite absent, as in some cases of *Ophrys*. . . . We can" (taking this view of the homology of the orchids) "understand the existence of the conspicuous central column; the large size, generally tripartite form, and peculiar manner of attachment of the labellum; the origin of the clinandrum; the relative position of the single fertile anther in most orchids, and of two fertile stamens in *Cypripedium;* the position of the rostellum, as well as of all other organs; and, lastly, the frequent occurrence of a bilobed stigma, and the occasional occurrence of two distinct stigmas."[1] In fig. 297 is shown a diagram of the flower of an orchid on the views of the illustrious naturalist quoted. With scarcely an exception, all of them require the aid of insects to fertilise them. To accomplish this, the most beautiful and elaborate contrivances exist in their varied flowers (about 6000 of them). The bee-master was for long acquainted with the fact that the club-shaped pollen-masses were carried by bees, from seeing them attached to the heads of these and other insects, but, it need scarcely be said, without understanding the import of it. To him it was only the "club sickness" (fig. 299). Within the last ten or twelve years an immense mass of facts has been accumulated on this subject, chiefly through the labours of Charles Darwin, and the school which his wonderful researches have stimulated into action. Almost every separate species has a different method of accomplishing its fertilisation through insect agency, but our space will only admit of giving two or three instances as specimens of the whole, referring the reader to the original sources, or to the plants themselves, for further information. The first method which we shall mention was communicated by Dr Crüger to Mr Darwin. In a species of *Coryanthes*, a tropical orchid, he "found that the labellum is hollowed into a great bucket, into which drops of almost pure water

---

[1] Fertilisation of Orchids, p. 294, 295, 301, 302.

continually fall from two secreting horns which stand above it, and when the bucket is half full the water overflows by a spout on one side. The bare part of the labellum stands on the bucket, and is itself hollowed out into a sort of chamber with two lateral entrances; within this chamber are curious fleshy ridges. The most ingenious man, if he had not witnessed what takes place, could never have imagined what purpose all these parts serve. But Crüger saw crowds of large humble-bees visiting the gigantic flowers of this orchid, not in order to suck nectar, but to gnaw off the ridges within the chamber above the bucket. In doing this they frequently pushed each other into the bucket, and their wings being thus wetted they could not fly away, but were compelled to crawl through the passage formed by the spout or overflow. Dr Crüger saw a 'continual procession' of bees thus crawling out of their involuntary bath. The passage is narrow, and is roofed over by the column; so that a bee, in forcing its way out, first rubs its

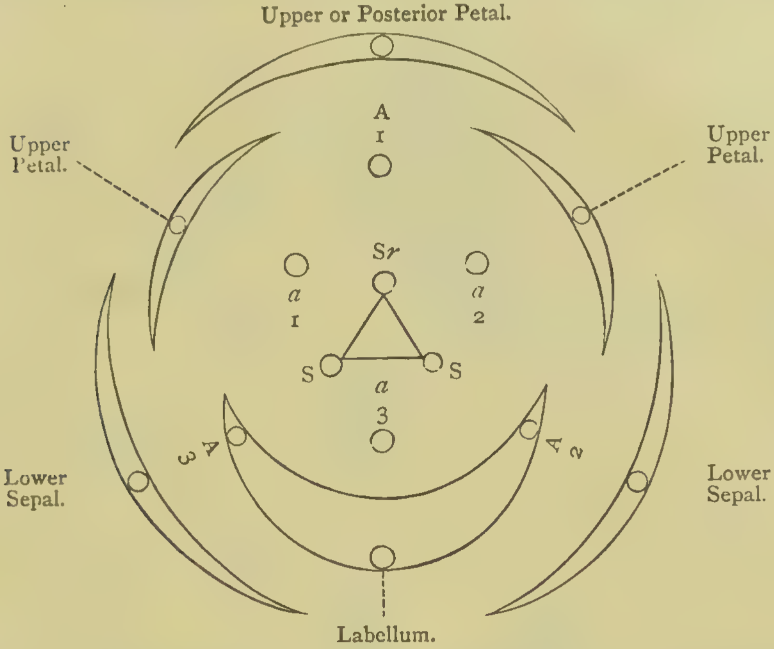


Fig. 297.—Section of the flower of an Orchid. S S, Stigmas; S *r* Stigma modified into the rostellum; A 1, Fertile anther of the outer whorl; A 2, A 3, Anthers of the same whorl combined with the lower petal, forming the labellum; *a* 1, *a* 2, Rudimentary anthers of the inner whorl (fertile in *Cypripedium*), generally forming the clinandrium; *a* 3, Third anther of the same whorl, when present, forming the front of the column. The fifteen little circles show the spiral vessels, which in every case can be traced down to the six large ovarian groups. They alternate in five whorls (as represented). In order to guide the eye, the three central groups running to the three pistils are connected by a triangle (after Darwin[1]).

---

[1] Orchids, p. 291, 292. See also Robert Brown in Trans. Linn. Soc., xvi. 696; Link, Bemerkungen über der Bau der Orchideen (Bot. Zeit., 1849, 745); Brongniart, Ann. des Sc. Nat., t. xxiv., &c.

back against the viscid stigma, then against the viscid glands of the pollen-masses. The pollen-masses are thus glued to the back

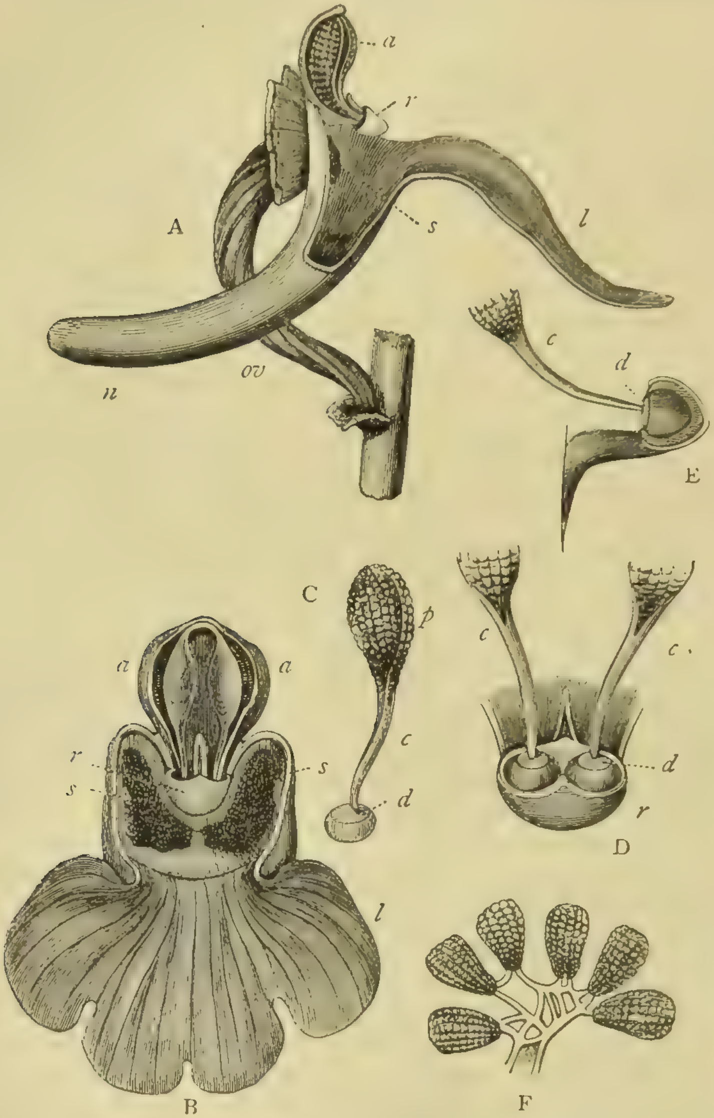


Fig. 298.—Anatomy of the flower of *Orchis mascula*, L. *a* Anther; *r* Rostellum; *s* Stigma; *l* Labellum; *n* Nectary; *p* Pollinium or pollen-mass; *c* Caudicle of pollinium. A, Side view of flower, with all the segments of the perianth cut off, except the labellum, of which the near half is cut away, as well as the upper portion of the near side of the nectary; *ov* Twisted ovary. B, Front view of flower, with segments of the perianth removed, except the labellum. C, One pollinium or pollen-mass, showing the packets of pollen-grains, the caudicle, and the viscid disc. D, Front view of the discs and caudicles of both pollinia within the rostellum, with its lip depressed. E, Section through one side of the rostellum, with the included disc and caudicle of one pollinium. F, Packets of pollen-grains tied together by elastic threads, here extended.[1]

---

[1] From a copy of a drawing by Franz Bauer in Darwin's Fertilisation of Orchids, p. 18.

of the bees which first happen to crawl out through the passage of a lately-expanded flower, and are thus carried away. . . . When the bee, thus provided, flies to another flower, or to the same flower a second time, and is pushed by its comrades into the bucket, and then crawls out by the passage, the pollen-masses necessarily come first in contact with the viscid stigma and adhere to it, and the flower is fertilised. Now at last we see the full use of every part of the flower, of the water-secreting horns, of the bucket half full of water, which prevents the bees from flying away, and forces them to crawl out through the spout and rub against the properly-placed viscid pollen-masses and the viscid stigma."[1]

Could anything be more extraordinary? And yet a hundred other such instances could be given. Not less interesting, though probably at first sight not so startling, is the arrangement in the common *Orchis mascula* of our damp pastures, which, with the aid of the figures given by Mr Darwin (fig. 298), and the description of the structure at p. 442 of this text-book, we may explain, as the plants can easily be obtained. Should an insect alight on the labellum—a good landing-place—and push its head into the chamber (fig. 298, A, or front view B), at the back of which lies the stigma (*s*), in order to reach with its proboscis the end of the nectary—or, which does equally well to show the action, push a sharply-pointed common pencil into the nectary — the result is that, "owing to the pouch-formed rostellum projecting into the gangway of the nectary, it is scarcely possible that any object can be pushed into it without the rostellum being touched. The exterior membrane of the rostellum then ruptures in the proper lines, and the lip or pouch is most easily depressed. When this is effected, one or both of the viscid balls will almost infallibly touch the intruding body. So viscid are these balls, that whatever they touch they firmly stick to. Moreover, the viscid matter has the peculiar chemical quality of setting like a cement, hard and dry, in a few minutes' time. As the anther-cells are open in front, when the insect withdraws its head, or when the pencil is withdrawn, one pollinium, or both, will be withdrawn firmly cemented to the object, projecting up like horns. The firmness of the attachment of the cement is very necessary, as we shall immediately see; for if the pollinia were to fall sideways or backwards, they could never fertilise the flower. From the position in which the two pollinia lie in the cells, they diverge a little when attached to any object. Now, let us suppose our insect to fly to another flower, or insert the pencil with the attached pollinium into the same or into another nectary (fig. 298, A), it will be evident that the firmly attached pollinium will be simply pushed against or into its old position—namely, into the anther-cell. How, then, can the flower

---

[1] Origin of Species, 6th ed., p. 154, 155.

be fertilised? This is effected by a beautiful contrivance. Though the viscid surface remains immovably fixed, the apparently insignificant and minute disc of membrane to which the caulicle adheres is endowed with a remarkable power of contraction, which causes the pollinium to sweep through about 90 degrees, always in one direction—viz., towards the apex of the proboscis or pencil —in the course, on an average, of thirty seconds. Now, after this movement and interval of time (which would allow the insect to fly to another flower), it will be seen, by turning to the diagram (fig. 298, A), that if the pencil be inserted into the nectary, the thick end of the pollinium will exactly strike the stigmatic surface. Here comes into play another pretty adaptation, long ago noticed by Robert Brown.[1] The stigma is very viscid, but not so viscid as, when touched, to pull the whole pollinium off the insect's head, yet sufficiently to break off the elastic threads (fig. 298, F), by which the packets of pollen-grains are tied together, and leave some of these on the stigma. Hence a pollinium attached to an insect, or to the pencil, can be applied to many stigmas, and will fertilise all. I have seen the pollinia of *Orchis pyramidalis* adhering to the proboscis of a moth, with the stump-like caudicle alone left, all the packets of pollen having been left glued to the stigmas of the flowers successively visited" (fig. 299). The balls of viscid matter within the pouch-formed rostellum are surrounded with fluid, which is important, as the viscid matter sets hard when exposed to the air for a short time. Various other similar smaller contrivances, as noticed by Darwin, might be mentioned. For instance, the pouch, after being depressed, springs up to its former position: and this is of the greatest service; "for, if this did not take place, and an insect, after depressing the lip, failed to remove either viscid ball, or if it removed one alone, in the first case both, and in the second case one, of the viscid balls would be left exposed to the air; consequently they would quickly lose all adhesiveness, and the pollinia would be rendered absolutely useless."[2]

Fig. 299.—Head and proboscis of *Acontia luctuosa* (a moth), with seven pairs of the pollinia of *Orchis pyramidalis* attached to the proboscis (after Darwin).

In *Catasetum*, another orchid closely allied to *Coryanthes*, the

---

[1] Trans. Linn. Soc., xvi. 731 (Miscell. Bot. Works, i. 534).

[2] On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing (1862), p. 14-19.

structure of the flower is widely different, though serving the same purpose, and is equally curious. According to Mr Darwin's description, bees visit these flowers, like those of Coryanthes, in order to gnaw the labellum. In doing this they inevitably touch a long tapering sensitive projection, the "antenna" of the rostellum. This antenna, when touched, transmits a sensation of vibration to a certain membrane around the whole exterior surface of the rostellum, which is instantly ruptured; this sets free a spring, by which the pollen-mass is shot forth like an arrow in the right direction, and adheres by its viscid extremity to the back of the bee. The pollen-mass of the male plant (for in this orchid the sexes are separate) is thus carried to the flower of the female plant, when it is brought into contact with the stigma, which is viscid enough to break certain elastic threads, and, retaining the pollen, fertilisation is effected.[1]

In the Lady's slipper (*Cypripedium*), of which we have one rare native species (*C. Calceolus*, L.), but many exotic ones are in our conservatories, the plan of fertilisation is so very different from that of any of the Orchis family, that, even at the risk of infringing on the space allotted to other departments of vegetable physiology, we must describe it in the words of Dr Gray, not having seen the action ourselves. In *Cypripedium spectabile* of the Northern United States, unlike other orchids, there are two stamens; the pollen is powdery, or between powdery and pulpy, and not very different from that of ordinary flowers. "As it lies on the open anther in a broad patch, it somehow gets a film-like and thin coat of sticky varnish. The stigma is large, flat, and somewhat trowel-shaped, the face turned forwards and downwards; it is supported on a short style, to which the anthers have grown fast, one on each side. This apparatus is placed just within the upper part of the sac or slipper (rather like an Indian moccasin than a slipper), which gives its name to the flower. There are three openings in the slipper: a large round one in front, and the edges of this are turned in, after the fashion of one sort of mouse-trap; two smaller ones far back, one on either side, directly under each other. Flies and the like enter by the large front opening, and find a little nectar apparently bedewing the long hairs that grow from the bottom of the slipper, especially well back under the overhanging stigma. The mouse-trap arrangement renders it difficult for the fly to get out by the way it came in. As it pushes on under the stigma, it sees light on either side beyond, and in escaping by one or other of these small openings, it cannot fail to get a dab of pollen upon its head, as it brushes against the film with which the surface is varnished. Flying to the next blossom, and entering as before,

---

[1] Origin of Species, 6th ed., p. 155.

as the insect makes its way onward it can hardly fail to rub the pollen-covered top of its head against the large stigma which forms the roof of the passage. The stigma of every other orchid is smooth and glutinous. This is merely moist and finely roughened. The roughness arises from very minute projections, all pointing forwards; so that the surface may be likened to that of a woolcard or of a rasp on a very fine scale. So, as the insect passes under, the film of pollen is carded or rasped off its head by the stigma, and left upon it; and when the fly passes out it takes a fresh load of pollen on its head with which to fertilise the next flower."[1]

Fertilisation of the Asclepiadaceæ.—The flowers of *Asclepias* are also fertilised by insects, though their flowers are hardly so complicated as those of orchids, and the pollinia are in pairs hanging by curved stalks from a dark-coloured disc. At the moment of fertilisation, the anthers of the Asclepiadaceæ, which are in a manner applied against the stigma, open, and the cellular envelope in which the pollen-grains are enclosed ruptures on the side nearest the stigma, and allows of the protrusion of a great number of pollen-tubes, which are identical in their nature with those emitted by the pulverescent pollen-grains.[2]

The flowers of some orchids resemble butterflies and moths (p. 442)—*e.g.*, *Oncidium*, *Papilio*, and *Phalænopsis*, &c.—and it is just possible that these forms may serve to attract insects, though, as already noticed, the bee orchis (*Ophrys apifera*) is, curiously enough, the only one which is capable of self-fertilisation. On the whole, looking at the manifold contrivances in orchids to enable insects to get entangled with the pollen-masses, a noble author is well justified in saying that—*mutatis mutandis*—the ancient warning of "spring-guns and *moth*-traps set here" might well be written over the flower of every species of that great order. The student who can witness all these wondrous forms, and their not less wonderful physiology, without seeing in plant-life a deeper significance than even his ordinary studies of organography would lead him to, may be very sure that he has mistaken his vocation, and had better turn to pursuits where scientific curiosity and reverential wonder in no way add to the amenity of his daily life.[3]

---

[1] How Plants Behave, p. 31, 32.

[2] Robert Brown on the Asclepiadeæ, in Miscellaneous Works, ii. 193-247.

[3] For further information, see the works of Darwin and Gray already quoted; a paper by Mr Darwin in Ann. Nat. Hist., 1872; Journ. Linn. Soc. Bot., vi. 77, 151, vii. 69, viii. 169; and Gardeners' Chronicle, 9th June 1860; another by Dr Rutherford in Trans. Bot. Soc., 1865; Mansel-Weale in Journ. Linn. Soc., xiii. 42-45, 1871; Ibid., 45-47; Ibid., 47-48; Ibid., 48-51; Trimen in Journ. Linn. Soc. Bot., ix. (1865) 144; Ogle, Pop. Sc. Rev., April 1870; and, more

Considering how important a part insects play in fertilising nearly all plants, even the homogamic ones (for though in these plants the stamens and pistils are present in one flower, it would be a mistake to say that, because they are capable of self-impregnation, this is accomplished in every case, for insects often complete what rain or unfavourable weather may have prevented), might it not be worth trying the value of the suggestion made more than seventy years ago by Willdenow, after the first publication of his friend Sprengel's observations, that when gardeners wish to make cherry or other fruit trees bear early in the season, when they often get little or no fruit at all, they should place a beehive with bees in the hothouse, and at the same time take care to let those busy insects get at as many flowers as possible?[1]

The Wind as a Fertilising Agent.—We have seen that nature trusts not alone to insects to accomplish this cross-fertilisation, but employs also inorganic agents. In Coniferæ, Amentaceæ with pendulous anthers, some Chenopodiaceæ with enormously superabundant pollen, passion-flowers, &c., with versatile anthers pendent from the extremity of a long filament, the wind assists in carrying the pollen from flower to flower; and as in these plants the pollen, instead of being viscid, is dry, this is easily accomplished. Perhaps the fact that in hazels and willows the pollen is distributed before the appearance of the leaves, or, as in the case of evergreens and in pines, is produced more abundantly, and meets with little obstruction from the smooth and circular leaves, may be also looked upon as further evidences of design to assist the winds in their office. Again, in many instances, where the wind performs the office of wafting the pollen from flower to flower, there is no corolla to hide the pistil; while the stigmas are downy or plumose, the better to intercept and retain the floating grains. At the same time, the interference of insects is checked by the absence of honey and of perfume.[2] In fact, in all the plants which Delpino has called Anemophilous, the wind wafts the pollen for fertilisation—a method of fertilisation which perhaps

---

particularly for the fertilisation of *Cypripedium*, a separate work by H. Müller, entitled Uber die Anwendung der Darwin'schen Theorie auf Blumen und blumen besuchende Insecten, 1870. The same author has discussed insect fertilisation very fully in Die Befruchtung de Blumen durch Insekten, und die gegenseitigen Anpassungen beider, 1873; Hart in Nature, Aug. 4, 1870; Scott in Trans. Bot. Soc., vii. 543, Journ. Linn. Soc., viii. 91; Bentham "On the Stigmatic Apparatus of Goodenovieæ," Journ. Linn. Soc. Bot., x. 293, &c.

[1] For the connection of insect fertilisation with the geographical distribution of plants, *see* PHYTO-GEOGRAPHY. The whole question of the agency of insects has been discussed by Hermann Müller in his recent work, already quoted, which contains a *résumé* of the now rather voluminous literature of the subject in German, Italian, Swedish, and English.

[2] Elliot in Trans. Bot. Soc., vi. 4.

Mr Darwin has rather underestimated. It is especially well seen in grasses.

Fertilisation of Grasses.[1] — The earlier observers — Morren, Naudin, and Bidard—believed that self-fertilisation was the rule among grasses. The more recent observations of Delpino and Hildebrand have, however, shown, that with the exception of those grasses the flowers of which never open, the agent of fertilisation is the wind, insects rarely visiting the flowers of these plants, and therefore playing but a minor part in the conveyance of the pollen from one to another. To facilitate this, the pollen-grains of grasses are in general rounded, smooth, and not attached to each other; so that as soon as the anthers open, they are discharged and dispersed through the air. In addition, the filaments of the stamens are, in most cases, long; so that the least breath of wind shakes out the pollen. The stigma is usually of a feathery character, presenting a large surface to the action of pollen, and provided, as Hildebrand points out, with a large number of hollows and projections, in and on which it may lodge. Still, though these contrivances render cross-fertilisation almost inevitable, self-fertilisation is not, as in orchids, absolutely prevented. The flowers of grasses only remain open for a short, for an extremely short time; and this, in different species, occurs at different periods of the day. Thus, for example, *Avena pubescens*—a species of wild oat—flowers only in the morning; *Ægilops cylindrica* and *Oryza sativa* towards noon; while *Phalaris canariensis* (canary-grass), the ordinary cultivated species of oat (*Avena*), and some other grasses, flower towards evening. The mode of fertilisation of these plants has therefore hitherto been overlooked. The state of the weather, by keeping the flower closed if the season is wet,[2] as among plants belonging to other orders, also determines the mode of fertilisation. With respect to the facts which have

---

[1] For a full account see Hildebrand, "Beobachtungen über die Bestäubungs verhältnisse bei der Gramineen," Monats. d. preuss. Akadem. d. Wiss. zu Berlin, Okt. 1872, p. 737-764; or abstract by Mr A. W. Bennett in the 'Gardeners' Chronicle,' March 15 and 22, 1873; also Delpino, "Sulla dicogamia vegetale e specialmente suquella del Cereali," Bolletini del Comizio agrario parmense, March and April, 1871; Ascherson, in Bot. Zeit., 1871, No. 26 *et seq.;* Spruce, Journ. Roy. Hort. Soc., Dec. 21, 1869; Wilson, Trans. Bot. Soc. Edin., vol. xi., May 1873, and Feb. 12, 1874 (Gardeners' Chron., March 21 and 28, 1874); Axell, Om anordningarna för de fanerogama växternas befruktning, p. 52 *et seq.*

[2] Observations made during the summers of 1872 and 1873 (also confirmed by Mr Wilson) show that oat flowers open almost as freely in wet or cloudy days as when exposed to a clear sky and bright sunshine, though individual plants may remain shut (while the neighbouring ones are open) during gloomy or rainy weather. Mr Wilson has observed that the upper flowers of the oat panicle are often in blossom before the lower are out of the sheath.

been absolutely determined, grasses may be classed under the following heads:—

(1.) *Diœcious Grasses.*—These are necessarily cross-fertilised, but are few in number. Ex. *Calamigrastos dioica*, *Guada dioica*, *Buchlöe dactyloides* (the American buffalo grass), &c.

(2.) *Monœcious Grasses.*—These are more common, and must always be, in the strict sense of the term, cross-fertilised. The maize (*Zea mays*) affords a good example of protrandrous monœcism, "the upper male flowers in the spike having often lost their pollen before the stigmas are protruded from the lower male flowers." On the other hand, *Croix lacryma* (Job's tears) affords an instance of protogynous monœcism.

(3.) *Polygamous Grasses.*—Here, though self-fertilisation is probable, cross-fertilisation may take place, as in the genera *Panicum*, *Arrhenatherum*, *Andropogon*, &c.

(4.) *Protogynous Grasses.*—In these grasses the stigma is extended from the closed paleæ long before the opening of the flowers or dehiscence of the anthers; and in only a very few cases is the stigma receptive beyond a brief period. Examples are afforded by *Anthoxanthum odoratum* (the vernal grass), *Alopecurus pratensis* (meadow foxtail), *Nardus stricta* (mat grass), &c.

(5.) *Grasses with Synchronous Development of Pistil and Anthers.*—(Homogamous or synacmic.)

(*a*) Even in these plants, in which self-fertilisation is not only possible but probable, cross-fertilisation is often favoured in preference to self-fertilisation—as, among others, in the common rye (*Secale cereale*), rice (*Oryza sativa*), and in wheat (*Triticum vulgare*), and other species of that genus. It is quite erroneous, as Delpino has shown, that wheat is necessarily self-fertilised. In a wheat-field not more than perhaps one in 400 of the flowers are open at one and the same time. The opening of the flower of wheat is a very interesting phenomenon, and happens with great rapidity. "While the flowers are still closed, a motion of the glumes is observable; these separate suddenly, in a moment; at the same time the anthers protrude laterally from the opening, open, and about one-third of the pollen falls inside the flower upon its own stigma, while the remaining two-thirds is dispersed into the air; the anthers are emptied in a moment, and the whole process does not last more than half a minute. The stigmas remain receptive for a considerably longer period, and can then receive the pollen of other flowers."

In rye the same acute observer shows that "the filaments elongate gradually; the anthers are extended between the apices of the paleæ, which are still nearly closed, and finally become free to their base, and are then tilted up laterally, thus projecting a portion of the pollen through a longitudinal slit which commences at the apex. At this period the flower is still almost entirely closed and the stigma unreceptive; so that this portion of the pollen which is first shaken out goes to the fertilisation of other flowers which are already open. Only after the tilting up of the anthers the two paleæ separate for several hours, the stigmas bend forward and become receptive, the slits in the anthers at the same time lengthen, and the rest of the pollen is then shaken out by the least breath of wind. A portion of this may fall on the pistil in the same flower, but by far the greater part, owing to the relative positions of the parts, is conveyed to other flowers. In *Secale montanum* the process is precisely similar."

(*b*) In others—such as *Briza maxima* (quaking grass) and *B. media* (darnel grass), *Cynosurus cristatus* (crested dog's-tail grass), *Hordeum jubatum*, *Lolium temulentum*, &c., the fact of the stigma and the anthers being mature at the same time, either protruded or in close flowers, and the filaments either stiff or bent round towards the anthers, renders cross-fertilisation and self-fertilisation possible to almost, if not quite, the same degree.

(*c*) Finally, in others—such as *Avena sativa*, *Bromus secalinus*, &c.—though self-fertilisation is favoured, it does not occur exclusively. The conditions of pollenisation or fertilisation must be observed in each species separately, since closely allied species of the same genus show startingly different phenomena in this respect, and even exhibit different behaviour, according to the different conditions of climate. The common *Poa annua*, a winter-flowering plant, is, for instance, self-fertilised; and in India the different varieties of rice remain constant, even though grown in an adjacent field, so that it would seem as if no crossing took place in this instance.[1]

---

[1] The observations of Mr A. Stephen Wilson, made in Scotland, do not thoroughly confirm those of Delpino and Hildebrand. In all except one variety of barley (*Hordeum distichon*, the golden or Italian barley) the flower opened during the act of fertilisation. This variety alone fertilises in an unopened flower, though the cause of this is still unknown. He considers that it is not rigorously proved that cross-fertilisation takes place in the cereal grains which he examined, and believes that though insects are certainly not the agents by which cereals are fertilised, yet that the wind is not an agency in this function in the same sense as it is in diœcious plants—"The essential agency is probably the sudden extension of the filaments, causing a few grains of pollen to be emptied out of the anthers before they are entirely ejected from the flower-cup." In some recent observations by the same experimenter, he remarks: "It seems to be the case that wheat, barley, and oats, whether they fully or but partially open their flowers, are fertilised before the anthers are visible outside. The coming of their anthers outside, or discharging a remnant of pollen in that position, is an accidental circumstance of no essential importance; while with rye an exterior discharge is always essential, but fre-

In the plantain or rib grass (*Plantago major*, *lanceolata*, &c.)—belonging, however, not to the order Graminaceæ, but to the order Plantaginaceæ—fertilisation must also be accomplished by means of the wind, as the flowers of these plants are, equally with those of grasses, unvisited by insects, and are protogynous.

Delpino — Professor of Natural History at the first school of Vallombrosa, but at present one of the scientific staff of the Italian circumnavigating expedition on board the Garibaldi—who has so identified himself with this subject of dichogamy, has suggested a convenient nomenclature to express the different methods in which this dichogamous fertilisation is accomplished. On this principle he divides plants into the following groups :—

(1.) The lower orders of plants, in which the mobile antheridia accomplish fertilisation without any intermediate agent, he calls *Zoogamous*, while the term (2.) *Diamesogamous* is applied to those which require such agency. This last section he divides into three subdivisions: (α) Hydrophileæ, (β) Anemophileæ, (γ) Zoïdiophileæ. The plants under the first heading (Hydrophileæ) are fecundated by the aid of the water in which they grow acting as the intermediate agency. Such are the Florideæ, the Naiadaceæ (notably *Posidonia caulini*, a kind of water-grass), *Ceratophyllum*, *Vallisneria*, &c. The second group (*Anemophileæ*) comprises Coniferæ, Amentaceæ, Negundo, palms, Urticaceæ, Euphorbiaceæ, many apetalous

quently a failure. The flowers are seldom open above half an hour ; and seldom are there more than three or four florets open at one time on a spike. 'It is generally believed,' says Mr Alfred W. Bennett (How Flowers are Fertilised, a Lecture, 1873, p. 11)—'though on this point further experiments are still wanting—that our cereal crops, especially wheat, rye, and barley, are fertilised exclusively by the agency of the wind. The flowers are small and uncoloured, without calyx or corolla ; the anthers are hung lightly on the end of long slender filaments ; the pollen is very fine and powdery ; and insects are hardly ever seen to visit them. Favourable weather (fine and sunny, with light breezes, and yet not so strong a wind as to disperse the pollen to too great a distance, so that it will not perform the purpose for which it was designed) at the time when the plants are in flower—*i. e.*, in the early part of June—is therefore of very great importance for the insuring of heavy crops.' But we have seen that the rule which applies to wheat, barley, and oats, does not apply to rye. We have seen, also, that the wind is entirely unnecessary to the fertilisation of wheat, barley, and oats. The Belgian farmers who trailed ropes over their flowering wheat, to insure complete fertilisation, were doing that which the very appearance of the anthers told them in whispers, not yet heard, had already been accomplished. The pollen of these plants, which the winds disperse, is not that which fertilises, but that which is not required for fertilisation. It is manifest that in the Italian barley, the largest-fruited of all the varieties, and which never opens its pales, nor disperses any pollen in flowering, cross-fertilisation has never taken place in all the lapse of its existence ; while in the case of the other barleys, wheats, and oats, even the florets which do fully open, are self-fertilised before space is afforded for the admission of neighbouring pollen."

genera, *Thalictrum* (one of the Ranunculaceæ), Polygonaceæ, and nearly all grasses. Fertilisation is accomplished by the wind carrying the pollen from one plant to another; while the third division (Zoïdiophileæ) are those in which fertilisation is accomplished by the aid of animals—insects chiefly—though the humming-birds may also aid in this work.

Fertilisation of Winter-Flowering Plants.—If insects are thus instrumental in effecting the fertilisation of plants, it may reasonably enough be asked, how can plants, which, like the gorse (Ulex Europæus) or the butcher's broom (*Ruscus aculeatus*), flower almost in mid-winter, or in early spring; or others, like the dead-nettles (*Lamium album* and *purpureum*), *Veronica Bauxbaumii*, daisy, dandelion, groundsel, common spurge (*Euphorbia peplus*), and others, which flower almost regardless of season or temperature, be fertilised? In the "dead season," when these plants are flowering, the number of insects which can assist in fertilisation is small indeed. Thanks to the interesting observations of Mr A. W. Bennett,[1] we are able to answer this question to some extent. He shows that in some of these plants at least, fertilisation, "or at all events the discharge of the pollen by the anthers, takes place in the bud before the flower is opened, thus insuring *self-fertilisation* under the most favourable circumstances, with complete protection from the weather, assisted, no doubt, by that rise of temperature which is known to take place in certain plants at the time of flowering." The truth of this is shown by the dissection of a flower of *Lamium album* (white dead-nettle), gathered in the last week of December (fig. 302), which "shows the stamens completely curved down and brought into contact with the bifid stigma — the pollen being at that time freely discharged from the anthers;" in *Veronica Bauxbaumii*, *V. agrestis*, *V. polita*, *Vinca major*, gorse, dandelion, groundsel, daisy, shepherd's purse (in which the four stamens appear to discharge their pollen into the bud, the two shorter ones not till a later period), *Lamium purpureum* (purple dead-nettle), *Cardimine hirsuta*, and *Stellaria media*, in which plant (the chickweed) the flowers open only under the stimulus of bright sunshine.

Fig. 300.—*Lamium Galeobdolon*, Crantz. Pistils and stamens from open flower, the latter discharging pollen (after Bennett).

---

[1] Nature, i. (1869) 11. We are indebted to Messrs Macmillan for the accompanying figures, originally prepared to illustrate Mr Bennett's paper.

On the contrary, in a few summer-flowering plants tempted by the mild winter weather to put forth a few sickly flowers, there was no pollen discharged before the opening of the flower, and no seed was observed to be formed. In *Lamium Galeobdolon*—or yellow archangel—notwithstanding its near relationship to the dead-nettle, the anthers did not discharge their pollen until after the opening of the flower (fig. 300). In some plants of warmer climates, which nevertheless flower in our gardens in winter, the pollen is not discharged until the opening of the flower. This is well illustrated in *Chimonanthus fragrans*, the "allspice tree," a native of Japan, which has a most perfect contrivance to prevent self-fertilisation (fig. 301). In a manner somewhat the same as Bennett has described in the "grass of Parnassus" (*Parnassia palustris*, p. 435),[1] "the stamens, at first nearly horizontal, afterwards lengthen out, and rising up perpendicularly, completely cover up

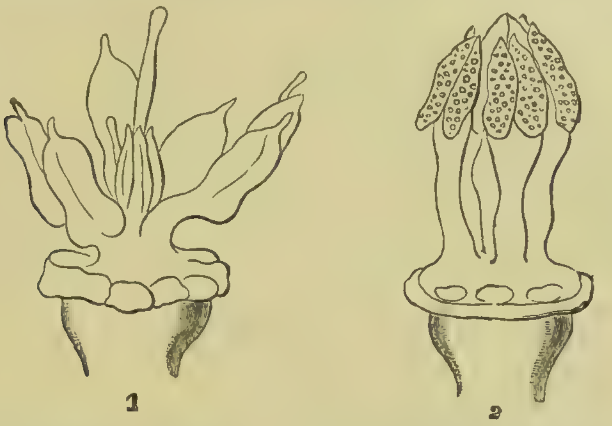


Fig. 301.—*Chimonanthus fragrans* (*N.O. Calycanthaceæ*). 1, Early stage of flower, calyx and corolla removed; 2, Later stage, stamens surrounding the pistil and discharging their pollen outwardly (after Bennett).

Fig. 302.—*Lamium album*, L. 1, Section of bud, calyx and corolla removed; 2, Stamen from bud, enlarged, discharging pollen (after Bennett).

---

[1] Journ. Linn. Soc. Bot., 1868-69, p. 24.

the pistil, and then discharge their pollen outwardly, so that none can possibly fall on the stigma." Accordingly, fruit is never produced in this country, though doubtless in its native climate it is cross-fertilised by insects. In diœcious winter-flowering plants this method of self-fertilisation in the bud cannot possibly take place. It is, however, accomplished—as in the case of the hazel—by the staminiferous catkins not only being in great number, but by the fact that each flower produces more stamens than the pistilliferous catkins, which are comparatively few in number. By this means the stigma runs every chance, amid the cloud of pollen discharged by the slightest breath of wind, of getting fertilised.

In the Euphorbias a single female flower is enclosed in a common envelope of involucral glands, along with a large number of male flowers—the flower being thus, though structurally unisexual, physiologically bisexual. In both the common winter-flowering species (*E. peplus* and *E. helioscopia*), the pistil makes its appearance above the involucral glands considerably earlier than the bulk of the stamens (fig. 303). "A single one, however, of these latter organs, was observed to protrude beyond the glands simultaneously, or nearly so, with the pistil, and to discharge its pollen freely on the stigmas, thus illustrating a kind of *quasi*-fertilisation. The remaining stamens do not discharge their pollen till a considerably later period, after the capsule belonging to the same set has attained a considerable size. In *E. helioscopia* the capsules are always included within the cup-shaped bracts, and the stigmas are turned up at the extremity, so as to receive the pollen freely from their own stamens." In the spring and summer flowering species, on the contrary, there is an arrangement for cross-fertilisation. It thus appears, from these interesting observations of Mr Bennett, which we have considered worthy of some space, even in the limited range of a text-book, that winter-flowering plants are self-fertilised in the bud; but that species

Fig. 303.—*Euphorbia helioscopia*, L. 1, Head of flowers opened, pistil and single stamen appearing above the involucral glands; 2, The same somewhat later, with the stigmas turned upwards (after Bennett).

which are properly summer-flowering, and only straggle into blossom in winter, have no such provision, but are either fertilised in the ordinary way or by means of insects.

CLEISTOGENOUS FLOWERS.

This term has been given to inconspicuous self-fertilised flowers, very different from the large and conspicuously-coloured ones found on the same plant in various species of *Impatiens* (*I. noli-me-tangere*, *I. fulva*, and *I. parviflora*). The two kinds of flowers are probably different in structure from the beginning, and the development of the two is entirely different. Self-fertilisation takes place in these "cleistogenous" flowers at a very early period, fruitful capsules appearing almost invariably to result from them; while in a vast majority of cases the conspicuous flowers are barren. If they are not barren, then the capsules contain the same average number of seeds as do those produced from the "cleistogenous" flowers. How these conspicuous flowers are fertilised is not known. As their structure appears to render self-fertilisation absolutely impossible, it is probable that this is accomplished by the wind or by insects, though there seems little to attract insects, and none have as yet been seen to visit these flowers. As Mr A. W. Bennett has remarked, it would, however, be strange if so handsome and complex a flower has been constructed without any benefit thereby resulting to the species.[1]

FERTILISATION OF WATER-PLANTS.

A well-known diœcious plant is *Vallisneria spiralis*, L., which, in many European canals, ditches, and lakes, grows in such abundance as seriously to impede navigation. It is one of Delpino's *hydrophileous* plants (p. 455). The male flowers are "very small, and united in a little spadix, shortly pedunculated, which is embraced by a spathe of two valves." The female flowers are, on the contrary, much larger, and at the end of a long peduncle, which is capable of elongating still further to enable the flower to reach and float on the surface of the water.

---

[1] For a full account of the structure and physiology of these cleistogenous flowers in one of the British species (*I. fulva*), the student is referred to an exhaustive paper by Mr Bennett in the Journ. of Linn. Soc. Bot., xiii. (1872) 147, t. 3: and for general details, to Mohl in Bot. Zeit., 1863; Gray's Genera Floræ Am. bor-orientalis; and Seemann's Journal of Botany, i. 147 ("Dimorphism in the Genitalia of Flowers"); Weddel in Jussieu's Monographie des Malpighiacées (*teste* Bennett), &c.

Shortly before the period of fecundation the male flowers detach themselves, and reaching the surface of the water, there perfect the development of their pollen, and float about until they reach the female ones. Fertilisation accomplished, the spiral peduncle of the female flower again contracts, and draws the fecundated plant to the bottom, where it matures its fruit and seeds. *Lagarosiphon muscoides*, an African plant, is fertilised in a very similar manner. Submerged water-plants, though developing their flowers and fruit beneath the water, invariably rise to the surface to perform the act of fecundation. In *Aldrovandra vesiculosa* and the water-soldier (*Stratiotes aloides*), for instance, the vesicular leaves, full of air-cavities, perform this buoying-up function. In *Ranunculus aquatilis* and *Alisma natans* the perianth becomes vesicular at the season of reproduction. In *Trapa natans* it is the petiole which becomes vesicular (p. 159); and in *Utricularia*, special buoys in the shape of little ascidia or bladders perform this good office (p. 158). In *Zostera*, or sea-grass (p. 346), the herbaceous spathe which encloses the flowers gets filled with air; while in *Nymphæa*, and other water-lilies, the peduncle which bears the flowers lengthens in proportion to the depth of water, in order to bring the flowers to the surface to fecundate.

PARTHENOGENESIS.

Th. von Siebold described certain insects belonging to the genus *Aphis*, which he affirmed could produce fertile eggs for several generations, without there being in each case direct generation, and to this phenomenon he applied the name *Parthenogenesis*[1] — a term which some botanists have retained to describe the production of seed without the fecundation of the ovule, which they affirm occurs in certain plants, notwithstanding the mass of facts which seem to prove incontestably the sexuality of plants. As early as last century, Spallanzani was led to believe that hemp, spinach, &c., could produce seeds without fecundation by the male plant; and since then various observers, among others Fresenius, Franz Bauer, Marti, Serafino, Volta, Girou de Buzareingnes, Ramisch, Bernhardi, Tenori, and more lately Liebmann, Gasparrini, Lecoq, Klotzch, Thuret, and Naudin, have hazarded their opinion of this existing in some unisexual plants. However, none of the plants which they described as showing this phenomenon—hemp, spinach—would bear strict investigation,[2] until, in 1829, Allan Cunningham sent to the Kew Gardens, from Australia, a euphorbiaceous plant—*Cœlebogyne*

---

[1] παρθένος, virgin; and γένεσις, generation.

[2] John Smith, Linn. Trans., xviii. 510.

ilicifolia—which for long was thought to show true Parthenogenesis. It produced female flowers which matured true seed, from which were raised other plants sent to the various botanic gardens of Europe, and these in their turn produced female flowers, no male plants being in Europe—nor could the slightest trace of stamens be detected.[1] Braun, Radlkofer, Schenk, and Regel, however, from their studies of the plant, began to doubt the existence of true Parthenogenesis in *Cœlebogyne*, until, in 1857, Baillon announced that he had found in the plant in the Paris garden a stamen at the base of the pistil, which assertion was formally denied by Decaisne, who affirmed that Baillon had mistaken for a stamen a glanduliferous bract. Finally, in 1860, Karsten settled the dispute by affirming that after studying the plant for two years in the Berlin Botanic Garden, he had come to the conclusion that the fifth flower on the plant was hermaphrodite; that there had existed on that plant two hermaphrodite flowers during the course of the summer, from the beginning of May to the end of August,[2] each containing a single stamen placed at the peripheral part of the flower, and containing a spherical pollen. Thus, in the present state of our knowledge, there is little or no ground for believing that any plant exists which can produce true seed susceptible of germination without fecundation—unless, indeed, the fig be taken as an example, Gasparrini having asserted that figs developed in summer never contain male flowers, but nevertheless produce seeds which contain an embryo.[3] Might they not be fertilised by means of insects or otherwise? Yet this careful observer considered that he had taken proper precautions against this method of fertilisation.

It may also be noted, that still more recently—viz., in 1863—the late Dr Thomas Anderson stated[4] that he observed in the Botanic Gardens of Calcutta a plant of *Aberia cafra* with pistillate flowers, in none of which could he, after two years' observation, discover a single stamen. Nevertheless the tree fruited, and the seeds produced vigorous plants. Still, as this tree might be visited by insects laden with the pollen, if not of this species, yet of others closely allied, the mere facts quoted, especially in the present state of our knowledge of hybridisation, are not sufficient to cause us to throw aside the vast accumulation of proofs in favour of the sexuality of plants, or even to affirm—*sub judice lis est.*[5]

---

[1] As shown by Achille Richard, Desfontaines, and even by Marti and Volta.

[2] Ann. des Sciences Nat., 1860, xiii. 254-287.

[3] Ibid., 3e sér., v. 206, xi. 365; also Radlkofer on Parthenogenesis, Ann. Nat. Hist., 1857; Regel, ibid., 3d ser., iii. 100; &c.

[4] Journ. Linn. Soc., vii. 67.

[5] For further information, see Bernhardi, in Otto and Dietrich's Allgemeine Garten Zeitung, 1839; Ann. des Sc. Nat., sér. 2e, xii., sér. 4e, i.; Annals of Nat. Hist., vii.; and Liebmann Proc. Linn. Soc., 1850.

SUMMARY.

The following table exhibits a classification of plants according to their method of fertilisation :—

I. HOMOGAMOUS PLANTS = Synacmic (Bennett) plants, in which the stamens and pistils are ripe about the same time. Homogamous plants may be—

1. **Hermaphrodite**, when the stamens and pistils are on one flower and ripe at the same time, when the fertilisation is *orthogamic* (p. 281).

2. **Monœcious**,[1] when the stamens and pistils are on separate flowers, but one plant (p. 281).

3. **Diœcious**, when the stamens and pistils are on separate flowers on separate plants (p. 282).

4. **Polygamous**, when the plant has mixed flowers (p. 282).

II. HETEROGAMOUS PLANTS[2] = Heteracmic (Bennett, *partim*), comprising all methods not homogamous.

It may comprise—

1. **Dichogamous Plants**, in which the stigma is not ripe at the same time as the anther is. These, again, may be—

(α) *Protandrous* = Dichogamia androgyna (Sprengel), in which the anthers are ripe before the stigma (p. 433).

(β) *Protogynous* = Dichogamia gynandra (Sprengel), in which the stigma is ripe before the anther (p. 433). These two methods Mr Bennett has comprised under the term *Heteracmic*. A Dichogamous plant may be monœcious, diœcious, or polygamous. A hermaphrodite plant is frequently so also.

2. **Dimorphic Plants**, when two of the stamens are long and two short (p. 428).

3. **Trimorphic Plants**, when the stamens are of three different lengths (p. 428).

4. **Cleistogenous Plants**, in which the inconspicuous flowers are self-fertilised in an early stage, and are markedly different from the conspicuously-coloured ones found on the same plant (p. 459). Finally, there may be added to all these—

5. **Parthenogenetic Plants**, in which it is said that seeds can be produced without the application of the pollen (p. 460).

---

[1] As a rule, monœcious and diœcious flowers are not homogamous, but it is not impossible for them to be so. More usually, however, they are heteracmic.

[2] Unfortunately, the term is applied by Maxwell Masters (Veg. Terat., p. 190) in a different sense—viz., to any cases in which the reproductive organs have a different arrangement from the habitual one.

In whatever way impregnated—orthogamically or heterogamically—the end is simply the production of the fruit and its contained seeds. To this end is the life of the plant directed. It is the alpha and omega of purely vegetable existence. All the other functions and organs only tend to the production of the seed, and the reproduction and continuation of the individual and the species. Our next studies must therefore be directed to the consideration of the product of the fertilised ovules,—treating previously, however, of the vessel in which they are contained—viz., the ripe ovary or base of the pistil, which now takes the name of the FRUIT.

CHAPTER X.

THE FRUIT.

As "all roads lead to Rome:" so no matter how the ovules are fertilised—whether orthogamically or heterogamically—the result is the same,—viz., the pistil swells and increases in size, and becomes the *fruit;* while the ovules in like manner grow and become *the seed.* To the latter organs the next chapter will be devoted. In the present one, we propose considering the mature pistil or fruit, its general character, structure, and different forms.

GENERAL REMARKS.

An exception to the general rule that the fruit is not matured until after the fertilisation of the ovules, is afforded by the Corinth grape (from which currants are made) and the St Michael orange: hence these fruits are almost seedless; or in other words, the seeds are in the form of ovules, if the oranges are taken before the latter are mature. The fruit, then, in the language of the botanist, is simply the matured pistil, or the seed-vessel and the seed—though, for the sake of convenience, we will consider the seed-vessel as the fruit, and so describe it under that head. In botanical language, a fruit need not be edible so long as it is the matured pistil. In some cases it is hardly recognisable in the popular eye as such.


Fig. 304.—Strawberry, showing the little fruits on the swollen peduncle, and the persistent calyx.


Fig. 305.—Strawberry, cut longitudinally.

An exception to the almost universal rule that the fruit matures itself in the air, is afforded by the ground-nut (*Arachis hypogea*) and *Trifolium subterraneum*, both of which, after fertilisation, bury themselves in the ground; and if anything intervenes to prevent this, the fruit does not mature, but withers away and dies.

Like the pistil, of which it is simply an enlarged edition, the fruit may consist of one carpel or of several, or of several carpels all coalesced, or of several carpels separated one from another; in other words, it may be *syncarpous* or *apocarpous*. The number of carpels entering into the composition of the fruit may be detected by the number of stigmas on the top: if there is only one, then only one carpel enters into the composition of the fruit; if more than two, three or a greater number make it up.

There are various forms of fruit, popularly so called, which properly have no correct claim to that distinction, or which do not come within the definition of the fruit which we have given. In the rose, for instance, the fruits are the seed-like bodies (achenes) concealed within the "hip"[1] (figs. 157, 158, p. 302). In the apple and pear the carpels are entirely within the edible portion of the fruit, which is a much swollen calyx and peduncle combined—the remains of the calyx being on the top of the fruit so called. In a strawberry, the fruits are the little seed-like bodies lying on the top of a swollen juicy peduncle, which is the real edible portion. Each of these carpels is surmounted by a style, even when the strawberry is ripe.

Among other forms of true fruits are the cherry and peach, in which the middle portion of the seed-vessel (pericarp) is pulpy and fleshy, while the third or innermost is hard and woody—this "stone" enclosing the true seed within it. In the raspberry and bramble (fig. 306) we see a collection of little stone fruits all arranged on a raised receptacle; while in the gooseberry and grape we see another form in which the pericarp is fleshy, and the seeds are embedded in a pulpy mass. We mention these examples to show the varieties which the fruits assume. These and numerous other forms will be again spoken of when we describe the various kinds of fruits in a systematic manner.

Fig. 306.—Ripe Bramble (*Rubus fructicosus*, L.), showing stone fruits on a common receptacle, and the persistent calyx (*s*). Each carpel is surmounted with the remains of the style.

PARTS OF THE FLOWER ADHERENT TO THE FRUIT.

The seed-vessel, which constitutes the bulk of the fruit, is called the *pericarp*;[2] and being only the matured pistil, ought to have the same structure as that organ. In general it has, but still there is usually some change which compels us to describe it

---

[1] The so-called *cynarrhodum* or *cynarrhodon*.

[2] περι, around; καρπος, fruit.

separately. In *Gymnosperms* (Conifers, Cycads) there is no pericarp, while in all *Angiosperms* there is. After the ovules have been fertilised, the life of the plant becomes concentrated in them and in the fruit generally, and the style and stigmas soon fade and die. In some plants they remain attached to the fruit in a shrivelled condition; while in other cases they not only remain fleshy, but even take a new development, and become a marked addition to certain fruits—*e.g.*, *Geum urbanum*, anemones, and *Clematis* (fig. 308), in which each fruit or carpel is terminated by a long feathery appendage, which is simply a special development of the persistent style (p. 359).

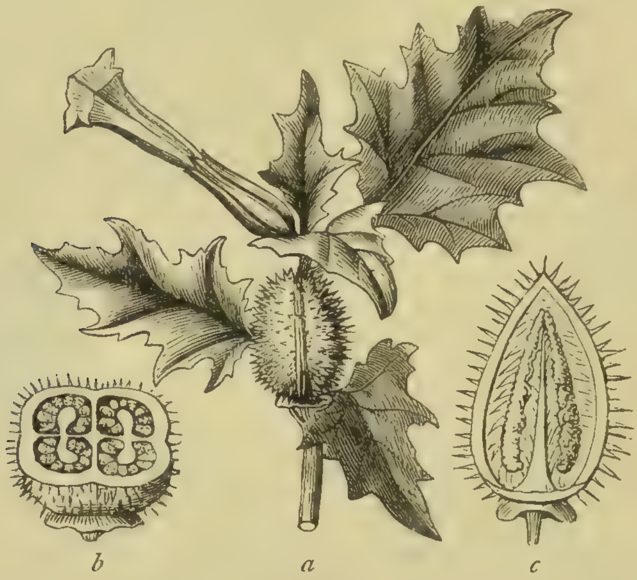


Fig. 307.—Thorn-apple (*Datura Stramonium*). *a* Plant showing leaves, flower, and fruit; *b* Transverse section of the fruit, and *c*, longitudinal section of the same, both showing the frill-like remains of the persistent calyx.

The calyx is the most general of all the floral verticils, but it does not often take any marked development, though, as in the strawberry (figs. 304, 305), *Geum*, or in the thorn-apple, where it partially persists, like a ruff or frill, under the fruit (fig. 307, and fig. 244, p. 353). In the apple, the greater part of the fleshy or edible portion must be looked upon as due to an increase of the tube of the calyx, which, in this case, has become fleshy (fig. 309). In the mulberry (*Morus*), the calyx gets united with each of the little fruits forming a part of it; while in the bramble (fig. 306), the calyx remains perfectly distinct from the fruit, which is therefore only like that of the mulberry in *general* appearance.

In *Gaultheria* the calyx becomes to all appearance a part of the fruit (p. 301); the real fruit is, however, a dry pod within. In *Blitum* (the "strawberry blite")—a member of the order Chenopodiaceæ—the fleshy calyces of a head of flowers, "each surround a small seed-like fruit, and together form a false multiple fruit, resembling a strawberry;" while the *induvium* of the winter cherry (p. 302), though seemingly a pericarp, is simply a fleshy calyx. Finally, in *Mirabilis* the calyx remains around the fruit in the form of a dry envelope.

Fig. 308.—*Clematis erecta*, L. Group of fruits with the terminal appendix, consisting of a development of the persistent style (nat. size).

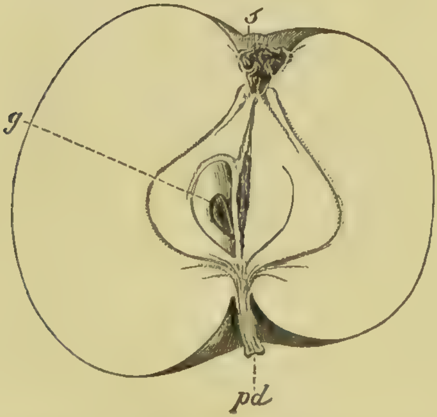


Fig. 309.—Longitudinal section of an Apple, showing the persistent calyx, more or less dried up (*s*), its peduncle (*pd*), and one of the seeds or "pips" in position (*g*).

Fig. 310.—Longitudinal section of the Fig (*Ficus carica*), showing the fruits enclosed by the fleshy conceptacle, which is only an enlargement of the peduncle (*p*).

Parts exterior to the fruit simulating the fruit.—In the fig, the peduncle swells up and surrounds the seed-like fruits inside, leaving only a hole exteriorly (fig. 310, and fig. 283, p. 297). In the Anacardiaceæ—for example, *Anacardium occidentale* and *Semecarpus Anacardium*—the "fruits," which are valued for their pleasant acidulous flavour, are only the swollen peduncles. In *Hovenia dulcis*, one of the finest of Japanese fruits, the edible portion is also the swollen peduncle.

In the wig-tree (*Rhus cotinus*)—so called from its hairy peduncles—some of the peduncles are simple and bear fruit, while others branch much and are sterile (fig. 142, p. 284). In the pine-apple (*Anassa sativa*, Lindl.) the edible fruit is of a very complex character. It is a "reunion of a great number of fruits properly so called, or pericarps, in which the seeds are abortive—conjoined with the bracts of the flowers which are found interspersed in the flower to the number of one median and two lateral ones for each—and which thus become succulent" (fig. 311).


Fig. 311.—Pine-apple (*Anassa sativa*, Lindl.)

These preliminaries are necessary to a right understanding of the structure of a typical fruit, in which the *pericarp*, or matured wall of the ovary which encloses the seed, is composed of three layers. Previously, however, to describing this, it may be well to consider what changes the fruit has undergone from the time we last studied it as the pistil—in a word, the processes undergone in ripening.

RIPENING OF THE FRUIT.[1]

The ovary, during the process of maturation, which ends in its being transformed into the fruit, becomes in general sappier

---

[1] Duchartre, Éléments de botanique, p. 647; Lindley, Elements, vol. ii.; Couverchel, Ann. de Chimie et de Physique, xlvi. 147; Fremy, Comptes rendus, vol. xix., 1784; Ann. de Chim. et de Phys., sér. 3, xxiv.; Journ. de Chim. Méd., 1845, p. 132.

and more swollen out, and the materials in the cells become considerably enlarged. In some cases, like that of the pod of the pea, the pericarp remains more or less crustaceous in texture, or becomes thin, dry, and membranous, like the Bladder senna pod (fig. 321). In such cases the pericarp is furnished with stomata, has chlorophyll in its cells, and in other respects acts like an ordinary leaf. In other cases we have seen the pericarp thicken (as in the gooseberry, date, &c.), or become hard and dry like a nut. In the case of the cherry, plum, peach, &c., the outer layers of the pericarp remain soft and pulpy, while the inner one (endocarp) hardens, and forms the putamen or "stone," characteristic of "stone-fruits."

During maturation the fruits not only modify their texture, but also undergo certain other changes, which we may sum up in a few words.

Changes in the Tissues.—As far as the changes of the tissues are concerned, the chief modification is the multiplication of the cells of the mesocarp, or other portion, which become thickened, so as to form the pulp; while the fibro-vascular bundles become attenuated, modified, and finally almost undistinguishable as such in the midst of the pulp. On the other hand, a contrary course of development takes place in certain cells of the pulp, which become quite hard, as is familiarly seen in the gritty particles scattered through the fleshy portions of many varieties of pears. An analogous development of hard matter results in the stone of certain fruits.

Changes in Substance.—The change in the substance consists chiefly in the contents of the cells undergoing certain chemical changes, the general result of which is, that the amount of sugar contained in them becomes greater, while the acids, starch, and tannin proportionally diminish. The fruit, while still green, it may be remarked, decomposes CO_2 and emits O, like the leaves; but when it ripens, this chemical action on the atmosphere alters. In other words, CO_2 is given out, accompanied by a sensible rise of the temperature, while O is absorbed. Fruits are tasteless or slightly bitter at an early age, when, both in structure, chemical composition, and action on the atmosphere, they are almost identical with leaves. They are afterwards sour, from the production within their cells of acids, the chief of which are tartaric acid (as in grapes), citric (lemons, oranges, cranberry), malic (in apples, gooseberries, &c.) At this period they exhale little oxygen; it is even said that they inhale a little of this gas. Subsequently a slow oxidation takes place: tannin first, and afterwards vegetable acids disappear; while sugar becomes notably increased as the ripening goes on; and the fibrous and cellular tissues also diminish as the sugar increases, the latter substance being partly produced at the expense of the former. This is proved by the following table, from analyses by Bérard, of the amount of lignine found in one hundred parts of the fruit during the green and ripe states :—

	Green.	Ripe.
Apricots,	3.61	1.86
Currants (including the seeds),	8.45	8.01
Duke Cherries,	2.44	1.12
Green-Gage Plums,	1.26	1.11
Melting Peaches,	3.01	1.21
Jargonelle Pears,	3.08	2.19

Yet Buignet is in doubt whether this table of Bérard supports this view, and is of belief that the sugar is not derived from the starch, which he declares is not found in the green fruit, except in bananas, but from an astringent substance, "which forms a colourless combination with iodine." Be this as it may (and we are by no means sure of the soundness of M. Buignet's view), it is still open to doubt whether the lignine of the green fruit in reality decreases as it ripens, or whether the dilatation of the cellular tissue, and the consequent augmentation of the aqueous products, render it proportionally less without being absolutely so (Bérard). But it was found by Couverchel that the gummy, mucilaginous, and gelatinous matters are capable of being changed into sugar. Thus, if apple-jelly is treated with a vegetable acid and dissolved in water, a sugar analogous to grape-sugar is obtained.

Variations.—There are, however, some remarkable disparities in this respect. Thus, in apricots and pears, malic acid keeps diminishing while their fruits ripen; while in currants, cherries, plums, and peaches, that acid augments during the same period. In currants, cherries, plums, and pears, gum keeps diminishing; while in apricots and peaches it augments, and so on.

Changes in Green Fruits when Cooked.—When green fruits are cooked, a change somewhat similar to what we have mentioned takes place in the fruit by the chemical elements, particularly the acids and mucilaginous products, reacting one on another, and by the aid of heat being converted into sugar.

Along with sugar is also produced vegetable jelly or amyloid (of which bassorin, salep, and pectine are apparently modifications), which in its characters is intermediate between starch, dextrine, and cellulose, and "has nearly the properties of starch when this has been altered by hot water." When dry it is horny or cartilaginous; but when moist it swells up, becomes gelatinous, and is capable of being perfectly diffused in cold water. In the tubers of orchids, and in the almond, bean, and other esculent seeds, it abounds. In some fruits, oils (volatile or thick) accumulate during the process of ripening. The sugar produced is sometimes liquid, or in other cases partly concrete, as in the grape, fig, and peach.

Production of Sugar during Ripening.—To sum up, we may therefore say, in general terms, that the increase of sugar keeps pace with the ripening of the fruit. The following table, also compiled by Bérard,[1] shows this more graphically than the mere statement of the fact would do :—

	Green.	Ripe.
Apricots (a trace when young, afterwards),	6.64	16.48
Red Currants, ...	0.52	6.24
Duke Cherries, ...	1.12	18.12
Green-Gage Plums, . . .	17.71	24.81
Melting Peaches, ...	0.63	11.61
Jargonelle Pears, ...	6.45	11.52

The observations of Frehling upon grapes brings out the same fact. On the 29th August they yielded to analysis 5.4 per cent of sugar, and 3.1 of acids; on the 11th September there was present 10.3 per cent of sugar, and 1.6 of acids; while on the 7th October, when the grapes were ripe, they contained 12.6 of sugar, with 1.20 only of acid, the density of the juice being at these three periods respectively, 46°, 59°, and 66° of the areometer.

According to Fremy, pears and apples contain, before being ripe, pectose, which in the course of ripening, by the action of the citric and malic acids, is changed into pectine. When the fruit passes maturity, this pectine passes completely into the state of metapectine. On the other hand, unripe fruits contain at the same time with pectine a ferment, "pectose," susceptible of acting on the pectine. It is under the action of this ferment that this last-named substance turns into pectannic acid, and at a later period into pectinic acid. The acids in their turn act on the starch, so as to transform it into sugar.

When succulent fruits are ripe, the sugar in its turn is oxidised, and then a series of changes occur which finally culminate in the *rotting* of the fruits.

Changes from Bletting to Rotting.—The first change after the sugar in the ripe fruit has commenced to oxidate is called "bletting."[2] It is, in fact, the intermediate stage between maturity and decay. The fruit, just before bletting sets in, is full of the materials we have already mentioned, and the plant is in a weak condition; for all we have said regarding the exhaustion of the plant

---

[1] Mém. sur la Maturation des Fruits, Ann. de Chim. et de Physique, sér. 2. xvi. 152, 225; *teste* Lindley, l. c., 256.

[2] A convenient word Anglicised by Lindley from the French *blessé*—a word signifying that peculiar bruised appearance we see in some fruits.

by flowering is true of fruiting in even a higher degree. The water, too, has diminished after the fruit is ripe, on account of the fruit absorbing less and less as it approaches maturity; and by the action of endosmose and exosmose the cell-contents are now of a tolerably uniform consistency throughout. De Candolle's description of this process is so clear that I will quote it in full: "After the period which is generally called that of ripeness, most fleshy fruits undergo a new kind of alteration—their flesh either rots or *blets*. These two states of decomposition cannot, according to Bérard, take place except by the action of the oxygen of the air, although he admits that a very small quantity is sufficient to cause it. He succeeded in preserving for several months, with little alteration, the fleshy fruits which were the subject of the foregoing experiments (apricots, currants, cherries, green-gages, peaches, pears), by placing them in hydrogen or nitrogen gases. All fruits at this extreme period of their duration, whether they decay or whether they blet, form CO_2 with their own carbon and the oxygen of the air, and moreover disengage from their proper substance a certain quantity of CO_2. Bletting is, in particular, a special alteration. This condition is not well characterised in any other fruits than those of Ebenaceæ (Ebony order, to which belong the Diospyros or 'persimmon' of the Southern United States) and the Pomaceæ (or apple order). Both these natural orders agree in having the calyx adherent to the ovary, and in their fruits being austerely sour before ripening. It would even seem, from the fruits of the persimmon, the sorb, and the medlar, that the more austere a fruit is, the more it is capable of bletting regularly. It has been found that a Jargonelle *pear* in passing to this state, loses a great deal of water (83.88 reduced to 62.73), a good deal of sugar (11.52 reduced to 8.77), and a little lignine (2.19 reduced to 1.85), but acquires rather more malic acid and animal matter. Lignine, in particular, seems in this kind of alteration to undergo a change analogous to that of wood in decay." The practical deduction from all this is, that if certain of the fruits named be kept in close vessels free of oxygen, they will preserve for a much longer period than they would otherwise do. Acidity may be corrected by exposure to light and air (as seen in cider-apples, which are sour until crushed and exposed to the air), and excessive sweetness or insipidity by diminution of light. In selecting wild fruits for cultivation, sour varieties should be selected, as it is the propensity of cultivation to develop sugar; and to render fruits at all well flavoured, a certain amount of acid requires to be present in the fruit.

Rotting is simply putrefaction—and putrefaction, M. Pasteur shows, commences by fermentation, this fermentation being in most cases produced by the germs of other plants. He comes to the conclusion that "there are two orders of life, one of which requires pure oxygen for its sustenance, while the other is killed by it. Apples, pears, cherries, gooseberries, currants, and the like, continue to live after being taken from the tree. As shown by Bellamy and Lechartier, they absorb and exhale CO_2, and ripen. Being prevented from absorbing oxygen, these fruits begin to assimilate oxygen from their own tissues, an alcoholic fermentation commences, and the fruit becomes soft and pulpy." Such, at least, are the views of this eminent French chemist.[1]

The Period required for the Ripening of the Fruit varies from a few days (as in the case of grasses, *Setaria viridis*, fescue-grass, *Briza media*, *Avena pratense*, *Aira cæspitosa*, &c., requiring from 13 to 17 days; while *Holcus lanatus*, *Elymus arenarius* (bent), and *Holcus odoratus*, require from 40 to 57 days) to a year or more (as in the case of Coniferæ). Most of our fruits require from 3 to 6 months, while the mistletoe takes 9 months to mature.

STRUCTURE OF THE PERICARP.

The pericarp is formed by the walls of the ovary, and most frequently determines the form of the fruit. Though greatly varying in size and thickness, the pericarp is present in all fruit, except those of gymnosperms, already mentioned. It varies in size, from a line to 2 or 3 feet, and is of all consistencies—fleshy, woody, horny, &c. When the fruit is composed of one carpel only, then, as a rule, the pericarp is very thin and closely adherent to the seed, so as to seem absent, or to cause the fruit to look like a seed. It was these kind of fruits, such as are found in Cyperaceæ (sedges) and Compositæ (fig. 156, p. 300), that the older botanists used to style, most erroneously, "naked seeds." Naked seeds, properly so called, are only found in Coniferæ and Cycads.

The *base* of a fruit is the point where it is united to the peduncle; while its *apex* or "organic *summit*" is the point where the style or stigma often remains persistent. If these are present they point out the summit of the fruit. In Helleboraceæ, Cruciferæ, poppies, &c., we see the style or stigma thus remaining. Hence, in those fruits where the style grows from the side, as in Labiatæ, Boraginaceæ, Rosaceæ, the organic and apparent summits are not the same. The structure of the pericarp, owing to the fact that it is a modified pistil, must be very much the same as that of a leaf, the pistil being only a metamorphosed leaf (p. 368). Ac-

---

[1] Pasteur, Comptes rendus, 1872; Trans. Quart. Journ. Mic. Sc., new series, xiii. 351; and for a summary of the same views, see Wyville Thomson, Trans. Bot. Soc. Edin., 1872.

cordingly, like a leaf, we find the pericarp composed of three layers.

1. The *outside* layer or epicarp, corresponding to the upper epidermis.

2. *Inside* layer or endocarp, corresponding to the inferior epidermis of the leaf; and

3. *Middle* or parenchymatous layer, which corresponds to the middle parenchyma or mesophyle of the leaf.

(1.) **Epicarp.**—This is a simple membrane, sometimes thin, at other times rather thick. It is easily torn off, as in the peach, cherry, or prune. In an inferior ovaried fruit, where it is adherent to the calyx, the epicarp is formed at once by the calyx and by the epidermis of the ovary fused into one membrane—*e. g.*, gooseberry, pomegranate, &c.

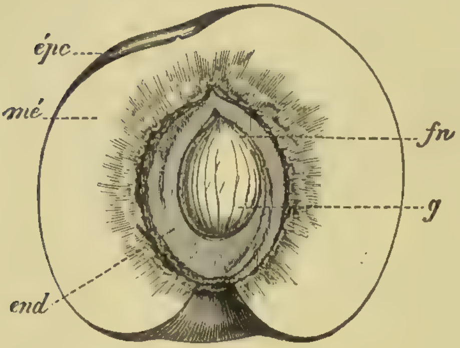


Fig. 312.—Longitudinal section of a Peach, (or the fruit of *Amygdalus Persica*, L.) *épc* Epicarp; *mé* Mesocarp; *end* Endocarp or stone, in the cavity of which is (*g*) the seed; *fn* Funiculus or cord by which the seed is attached (½ nat. size).

(2.) **Endocarp.**—This is the membrane which lines the cavity of each carpel when ripened into a fruit. It represents the epidermis or upper surface of the carpellary leaf. It is generally very thin and membranous. Sometimes, as in the pea, it takes the consistence of parchment; or it may become fused more or less with the nearest portion of the mesocarp, and become thickened; or even acquire a woody consistence, and become the *stone* or *putamen*, as in a peach, cherry, or prune (figs. 312, 313).

(3.) **Mesocarp.**—This comprises all the vascular or parenchymatous parts contained between the two membranes of the pericarp. It is extremely well developed in fleshy fruits,[1] constituting the edible portion or pulp, as in the peach, melon, &c. However, it is sometimes excessively thin, as in dry fruits, shell of the pea, wallflower, &c. But whether thick or thin it is always present, and the structure of the pericarp is the same.

There thus enter into the structure of the pericarp two membranes (the epicarp and endocarp) and a vasculocellar structure (the mesocarp). Pulpy fruits are no doubt, in the vast majority of cases, formed by the mesocarp. But this, we have seen, is not always so. In some cases (p. 49) the pulpy portion is formed by the calyx, either conjoined with the ovary or alone, as in the mul-

---

[1] Hence Richard calls it the Sarcocarp.

berry, roses, apple, and pine-apple. In other cases, in the juniper and yew, the *scales* become fleshy, and cover the seed in a more or less complete manner. This does not, however, constitute a true pericarp, which is the walls of the ovary, and is wanting in these gymnospermous plants. Lastly, the succulent portion of the strawberry, fig, &c., was supplied by the peduncle.

In the almond (fig. 313) we find a downy epicarp (*a*); a mesocarp thin but firm, and almost coriaceous; and all the remainder of the total thickness is made up of a thick stone or putamen (*b*), which is spongy in its middle portion. The mesocarp detaches itself from the stony endocarp at the period of maturity. The difference between the fruits of the peach and the almond, anatomically, is this, that in the one (peach) the mesocarp is fleshy, while in the other (almond) it is not. Yet this is but an unimportant difference; for in the variety of the almond called the Peach-almond (*Amygdalus communis*, L., var. *persicoïdes*), the stone is covered by a pulpy flesh which is edible (Duchartre).

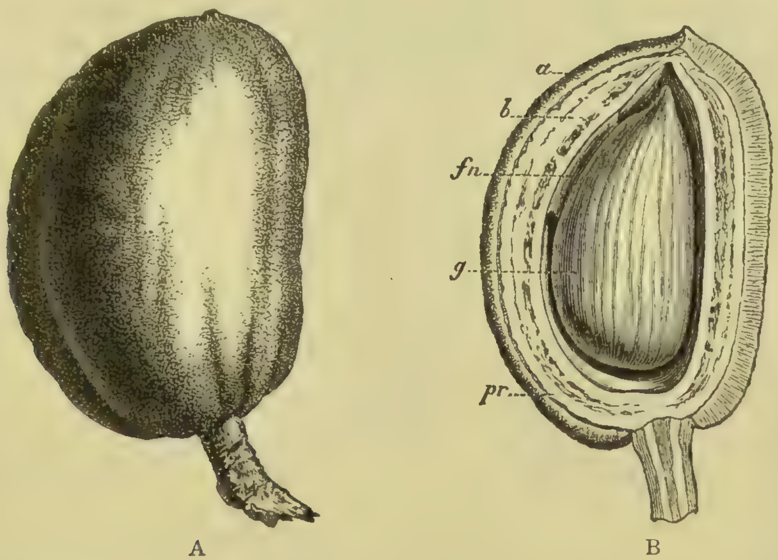


Fig. 313.—Fruit of Almond (*Amygdalus communis*, L.) A, Entire fruit. B, Longitudinal section: *a* Epicarp; *pr* Mesocarp; *b* Stone or *putamen* (endocarp); *g* Seed; *fn* Funiculus.

Loculaments or Cells and Dissepiments. — What we have already said on this subject in reference to the ovary (p. 352), to a great extent holds true in regard to the fruit. If the fruit is *simple—i. e.*, of one carpel—it will consist of a single loculament, or be what, in descriptive language, is called *unilocular.* However, as in the case of the ovary, the fruit may consist of several loculaments. Thus, that of the tobacco is *bilocular;* that of the flax *quadrilocular*; and so on—the term *multilocular* being applied if there are more than four.

Subdivision of Loculaments.—It may, however, happen, that an ovary may be unilocular, while the fruit may have two or more loculaments, by the form of partitions during the subsequent growth of the ovary. Take, for instance, the horned poppy (fig. 314). The ovary of this plant is unilocular, showing two parietal placentas, distinct and separate as usual. However, on making a section (fig. 314, B) on the long straight fruit (fig. 314, A), the result of an unusual increase in length of the ovary, we see that there has been produced between the two placentas a large spongy body, which unites them, and by the union divides the once unilocular ovary into a bilocular fruit. Duchartre points out the same peculiarity in several species of *Personia* (a genus of Proteaceæ). In like manner, while in the plants comprised in the tribe *Hedysereæ*, of the sub-order Papilionaceæ, of the order Leguminosæ, the ovary is unilocular, but by the bending in of the pericarp during the ripening process, the fruit is multilocular, each loculament containing one seed. Numerous similar instances might be quoted; but, as the two last examples, we may point out that in *Tribulus terrestris* the ovary is composed of five loculaments, each of which in the fruit is subdivided into three or four little cavities, each containing a seed; and that in the flax an ovary containing five loculaments has ten in the fruit, owing to the growth of false dissepiments in each loculament.

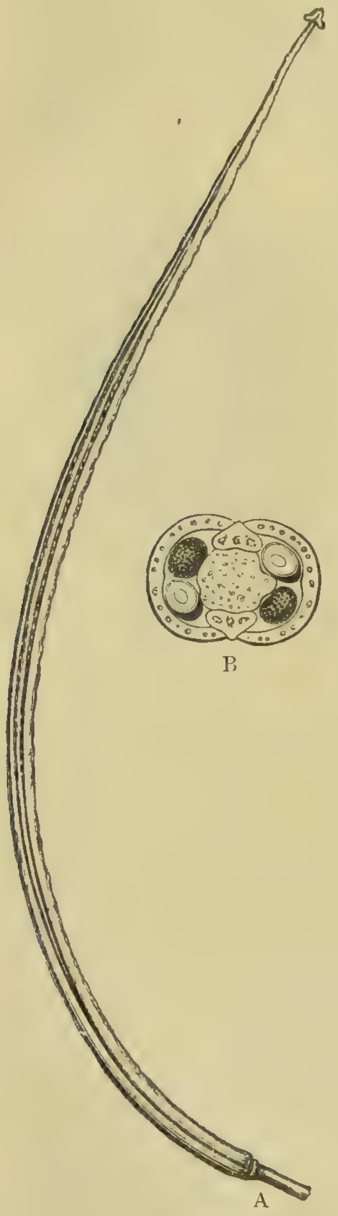


Fig. 314.—*Glaucium luteum*, Scop. A, Entire fruit (nat. size). B, Transverse section of the same (mag. 5 times).

Obliteration of Loculaments.—On the other hand, the number of loculaments in a fruit is not the same as in the ovary, from quite an opposite cause—viz., that frequently the dissepiments disappear, and a multilocular ovary may become *unilocular*, or with a smaller number of loculi than what the ovary possessed. In pinks and roses we often see this. It also affects the number of seeds contained in the fruit. Thus, in the olive order there are in the ovary two loculi, each containing two ovules; while there is in the fruit only one loculament containing one seed. In the oak, in like manner, the ovary is 3-celled, with two ovules in each cell; but the fruit is unilocular—the solitary loculament containing a solitary seed, owing to the non-development of two loculaments and five ovules. Exactly the same thing is seen in the hazel. In the cocoa-nut, again, a trilocular ovary becomes a unilocular fruit; while the bilocular ovary of the beech and elm produces in both cases a single seed of unilocular fruit—one of the ovules being abortive, while the other enlarges, breaks down the dissepiment, and so in time obliterates the empty loculament. The dissepiments, as in the case of the ovary (p. 352), may be either true or false. The same terms are applied to the placentas in the fruit as in the ovary (p. 563). If the pericarp is simple, then the placenta occupies each of the borders of the carpellary leaf, where they unite in a line or suture, as in the case of the pod of the pea, fruit of hellebore, &c.; hence such a placenta is called *sutural*, and so on. The position of the placenta is often extremely useful in characterising natural orders.

DEHISCENCE OF THE FRUIT.

The fruit, when ripe, must allow the seed to escape in order to enter the ground and germinate. In most stone-fruits, berries, &c., the fruit does not open, the seed simply falling out after the pericarp has rotted; while in the others the fruit opens in various ways when it is ripe. The opening of the fruit, to allow of the escape of the seed, is known as its *Dehiscence*. Fruits may therefore, in reference to this point, be divided into two great divisions,—the *Dehiscent* and the *Indehiscent*—those which open and those which do not. Dry fruits which have a single loculament and a single grain are generally indehiscent,—such as, for example, the fruit of the wheat (the wheat grain), barley, rye, and all the other grasses; the sedges, the Compositæ, &c.: while the same is true of the fleshy and succulent fruits—such as apples, pears, oranges, peaches, &c. To put it in other words — in capsules and berries the *seeds* are disseminated; in stone-fruits the stones contain the seeds; in *achenes*, or fruits where the thin pericarp is closely adherent to the seed (as in the wheat grain), the fruit is disseminated as a whole; while in a fourth case, the fruit breaks up into little pieces, each piece or *coccus* containing a seed, as in the Indian cress, Borage, *Platystemon*, &c. There are, however, exceptions even to the case of achenes being disseminated whole—for example, in *Oxalis* (sorrel), when, on dehiscence of the capsule, the elastic "testa" or "spermoderm" becomes ruptured, violently expelling the body of the seed with its covering (the "tegmen"). In the pomegranate, the fruits are swallowed by birds, and after digestion of the pulpy testa, the body of the seed, with the hard tegmen, is evacuated and disseminated. Or again, in such a drupe as an apple, where the induration of the endocarp is slight, we have the fruit behaving as a berry, dissemination taking place by means of seeds.[1]

When dehiscence takes place, the fruit breaks up into several pieces, regularly round its axis, or *columella*, when this is present, generally by valves, which constitute the walls of the pericarp. If the fruit is simple, or of one piece, it presents on the outside certain *sutural lines*, which mark the point where the free borders of each carpellary leaf unite. These lines are called *ventral sutures*, and each valve possesses one; while on the back of the valve there is another line—the *dorsal* suture—which corresponds to the midrib of the carpellary leaf. In a pea-pod, for example, the two sutures are equally well seen — one on the back and another on the front. When many carpels are soldered together by the greater part of their lateral aspects, in order to form a composite fruit, then the ventral sutures are found united in the middle of the fruit, and we see externally only the dorsal ones.

Hence most frequently the pericarp has double the number of sutures it has carpels, the valves by which it opens being equal to the number of carpels. Thus the pericarp of the tobacco-plant is composed of two carpels, and opens by two valves, or is *bivalvular*. In the tulip it is *trivalvular*, or composed of three carpels, and opens by three valves; that of the *Epilobium* is *quadrivalvular;* that of flax *quinquevalvular*, &c. In a unilocular fruit, made up of several carpels coalesced, the fruit dehisces by as many valves as there are carpels entering into its composition. Thus the fruit of the violet is unilocular, though made up of three carpels, and accordingly it dehisces by three valves.[2]

Taking up, therefore, dehiscent fruits, we may recognise several methods of dehiscence, which we will now briefly describe.

1. Porous Dehiscence, in which the seeds are liberated through holes or pores, which open when the fruit is ripe, near the upper end of the fruit. *Ex.* Poppy (fig. 315). This, though a method of liberating the seeds, is altogether different from valvular dehiscence, which, we have seen, is connected with the loculaments, and accordingly directly with the seeds; while this is simply rup-

---

[1] Alex. Dickson, Nature, August 31, 1871, p. 348.

[2] Richard, Nouveaux Eléments, 272.

turing, by which, as also in mignonette, snapdragon, and *Campanulaceæ*, a hole or holes are produced by the spontaneous absorption of a portion of the pericarp.

2. **Valvular Dehiscence,** in which the pericarp opens by valves. There are various ways in which this is done—viz.:

(*a*) *Loculicidal,* in which the valves open each along the line of its dorsal suture, and allow the seeds to escape. Ex. *Iris*, *Hibiscus*, evening primrose, and indeed most Monocotyledons, including the greater part of the Liliaceæ, Juncaceæ, Amaryllidaceæ, many Dicotyledons, such as Polemonaceæ, &c. (fig. 316).

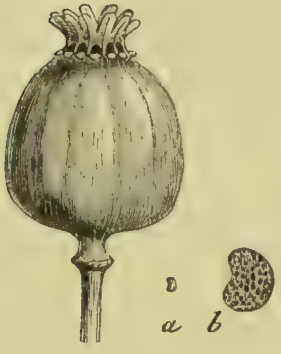


Fig. 315.—Fruit of the cultivated Poppy (*Papaver orientale*), with seeds (*a*, *b*, nat. size and magnified) illustrating porous dehiscence.

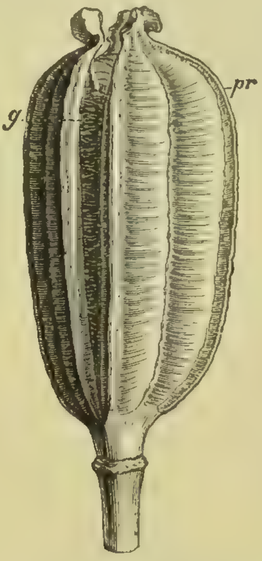


Fig. 316. — *Tulipa Gesneri*, L. Fruit, *pr*, opening by loculicidal dehiscence, allowing the seeds (*g*) to be seen.

(β) *Septicidal,* in which the fruit opens at the line of junction of the carpels. *Ex.* Azaleas, Rhododendrons, St John's wort (*Hypericum*), *Menziesia*, *Colchicum*, *Verbascum*, *Calceolaria*, *Scrophularia*, &c.

In some plants, such as chickweed, *Lychnis*, *Cerastium*, tobacco, pinks, and primroses, the pericarp only opens for a little way at the apex to allow the escape of the seeds. This variety of dehiscence has been called *apicular.* In the sea-pink (*Armeria*), however, we see such a gradation from the apicular to the septicidal as to justify us in considering this apicular dehiscence only a form of the one under consideration. It has sometimes been called the *denticidal*, or tooth-like dehiscence, from the teeth-like tips of the valves which surround the opening.

(γ) *Septifragal.*—In this form of dehiscence the valves fall away, leaving the dissepiments behind adhering to the axis. *Ex.* Fruits of the mahogany, and other Cedrelaceæ, *Hydrolea*, *Convolvulus*, &c. It is much rarer than the other two methods of valvular dehiscence.

3. **Circumcissal Dehiscence.**—In the rib-grass (*Plantago*), pimpernel (*Anagallis*), *Hibiscus*, *Lecythis*, or monkey-pot, &c., the seeds escape by the summit of the pericarp contracting in such a manner that it rises up in the form of a cap. Hence this is called transverse or circumcissal, and is remarkable, in so far that it has no connection with the line of union of the carpellary leaves (fig. 317). In the American genus *Jeffersonia*, the pericarp is only constricted half round, so that the summit is simply raised like the lid of a box, not lifted off, as is the usual way. The late Professor Hinks of Toronto considered that circumcissal dehiscence was due to the "force of cohesion of the parts of the circle, the absence of any of the causes favourable to dehiscence along the midrib of the carpellary leaf, and the operation of some force pressing either from without or from within on one particular line encircling the fruit."[1]

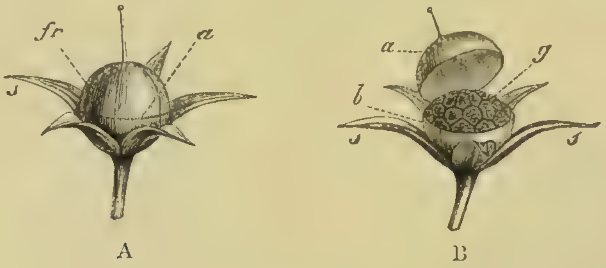


Fig. 317.—The Pimpernel (*Anagallis arvensis*, L.) A, Its entire fruit, *fr*, before dehiscence, and embraced by the persistent calyx, *s*; *a* Transverse, along which the pericarp dehisces. B, The same fruit, opening or divided into two hemispheres, *a* and *b*, of which the first (*a*) is raised up, allowing the seeds (*g*) to be seen (mag. twice nat. size).

Dehiscence of Unilocular Fruits.—Unilocular fruits, made up, nevertheless, of several carpels, may dehisce in the valvular manner exactly as if they were plurilocular. In some cases the septicidal dehiscence prevails, when the separate carpels of the unilocular pericarp open along the line where they meet or are attached to each other. In another form the loculicidal dehiscence is the rule, and the pericarp opens along the line of the dorsal suture of each valve, or carpellary leaf. In the pea, &c., the unicarpellary unilocular fruit, or pod, dehisces along the line of the ventral suture; such a mode of dehiscence in a simple fruit, such as the pea, being called sutural.

Elastic Dehiscence.—Some fruits in opening scatter the seeds with great force, thus affording one of the numerous methods by

---

[1] Annals of Nat. Hist., xvii.

which seeds are dispersed abroad to find a congenial soil at a distance from the parent plant, and thus better enable it to survive the "struggle for existence." In the ordinary *Balsamina hortensis* and *Lathræa Clandestina* we see this elastic dehiscence. But the best known, and not the least remarkable instance of it, is afforded by the squirting cucumber (*Ecbalium Elaterium*), which yields the elaterium of the *materia medica*. Detaching itself from its peduncle, the fruit suddenly contracts its walls, and forces out the seeds along with the liquid contents in the manner represented on fig. 318, and which peculiarity has given it its popular name.

Fig. 318.—*Ecbalium Elaterium*, Rich. Flowering and fruiting branch (*a*); *b* Fruit discharging its seeds.

In the sandbox-tree, the "Savilla" of the Hispano-Americans of the Isthmus of Panama, where it is found (*Hura crepitans*, L.), the fruit is composed of from twelve to eighteen carpels, partly coalesced, and with woody walls. These *cocci* (as carpels incompletely united among themselves by their sides are called) separate when the fruit is ripe, and open, each into two valves, with such force and noise that it has been likened to an explosion (Duchartre). Accordingly, in collections, the fruits of this plant, in order to prevent their opening, are generally firmly tied round with string, or even with iron wire.

CLASSIFICATION OF FRUITS.

The fruit being the mature pistil, will be as varied as the pistil itself; and accordingly, numerous names have been devised for these varied forms, by which the study of the fruit has hardly been simplified, but rather rendered such a chaotic mass of technical names, that *Carpology* has been dignified with the name of a science,—a science with all science left out—a field wherein the name-maker and the form-splitter have revelled, to the loss of others who view botany from worthier stand-points. Linnæus only used eight terms, which Gärtner[1] reduced to seven—adding, however, three secondary forms. Willdenow raised the number to seventeen, but defined them vaguely and inaccurately. Link, again, strove to reduce the number, and considered that eleven would have met the necessities of descriptive botany in his day. Richard proposed a somewhat more philosophical classification, though coining fresh names unknown to previous writers. Mirbel and Desvaux equally strove at distinguishing themselves in the same field, but with limited success—unless, indeed, running up the number of separate forms, as in Desvaux's case, to forty-three, be looked upon as such. The same may be said of the classifications of Lestiboudois, De Candolle, and Dumortier.[2] Indeed, the writers who have laboured in the fruitless field of fruit-classification are almost as numerous as the forms for which they have invented names.

Again was the voluntary task essayed by Lindley in 1848, with a success sufficiently great to allow his classification to be retained by most writers up to this date. It was, however, cumbersome, and burdened with many unnecessary names. He divided fruits first into the class **Apocarpi,** which comprises the *Utriculus*, *Achene*, *Drupe*, *Follicle*, *Legume*, and *Lomentum;* (2.) **Aggregati,** including the *Etærio*, *Syncarpium*, and *Cynarrhodum;* (3.) **Syncarpi,** including the *Caryopsis*, *Carcerulus*, *Samara*, *Amphisarca*, *Pyxidium*, *Regma*, *Conceptaculum*, *Siliqua*, *Silicula*, *Ceratium*, *Capsula*, *Hesperidium*, *Nuculanium*, *Tryma*, *Cremocarp*, *Glans*, *Cypsela*, *Diplotegia*, *Pepo*, *Balusta*, *Bacca*, and *Pomum;* (4.) **Anthocarpi,** or collective fruits, which embraced the *Diclesium*, *Sphalerocarpium*, *Syconus*, *Strobilus*, and *Sorosis*. It was an improvement on some of its immediate predecessors ; but, on the other hand, unnecessary terms were introduced, and a number which (like the *Tryma*, *Diplotegia*, *Amphisarca*, &c.) it is utterly impossible to clearly define. Since Lindley's day, carpological classification has been tinkered at by a number of botanists more or less qualified for the task. Schacht and Sachs, among others, have proposed classifications ; and that of the former eminent botanist has been emended with considerable advantage by Professor Alex. Dickson of Glasgow.[3] Most working botanists will, however, agree with Dr Maxwell Masters,[4] that much undeserved labour and refinement of nomenclature has been spent in trying to make a philosophical classification, and in devising terms which the exigencies of descriptive botany *might* require, but rarely or ever do. The truth is, that it is impossible to find a classification of

---

[1] De Fructibus et seminibus plantarum, 1788.

[2] Mem. de l'Acad. Roy. des Sc. de Bruxelles, vii. and ix.

[3] Nature, August 1871.

[4] Ibid., Nov. 2, 1871.

fruits which is founded on strictly scientific principles—the forms merging into each other; and to multiply terms to the extent which has been done, is simply to render the acquisition of the knowledge of the few forms which the student requires to be acquainted with intensely repulsive and difficult. In reality, if we examine the writings of the best living descriptive botanists (not themselves the authors of fruit-classifications)—Hooker, Bentham, De Candolle, Oliver, Baker, and others—we will find that they use very few carpological terms, modifying those in use by various adjectives, and so serving—what is the end of all organographical nomenclature—the purposes of systematic description, without resorting to the use of terms difficult to define, and at best vaguely applied. Accordingly, in the following classification, in which we have mainly followed Dr Masters, all the less easily defined forms are omitted, and the list reduced as much as possible, without at all destroying its usefulness. It is far from faultless; but we consider that its convenience and simplicity will atone for its "philosophical" imperfections.

MONOTHALMIC[1] FRUITS.

A. Ripe pericarp uniform.

Fruits indehiscent.—I. Nuts, or Achænocarps—viz., *Achene, Caryopsis, Carcerule, Glans, Samara, Nut.*

Fruits dehiscent.—II. Pods, or Regmacarps—viz., *Follicle, Legume, Siliqua, Capsule, Pyxis.*

B. Ripe pericarp, easily distinguishable into two or more layers.

Seeds within a hardened endocarp.—III. Stone-fruits, or Pyrenocarps—viz., *Drupe, Pome.*

Seeds embedded in pulp.—IV. Berries, or Sarcocarps—viz., *Bacca, Hesperidium, Pepo.*

POLYTHALMIC[2] FRUITS.

Fruits of several pistils on a common axis.—V. Cones, &c.—viz., *Strobilus, Sorosis, Scyonus.*

I. (1.) **Achene.**[3]—This is a dry, indehiscent, one-seeded, seed-like fruit, composed of a wingless solitary carpel, in which the pericarp

---

[1] μονος, one; and θαλαμος, bed: fruits formed from one pistil.

[2] πολυς, several; and θαλαμος: fruits formed from several pistils.

[3] *Achenium* of authors; *Akena* (Necker), *Stephanoum* (Desvaux), *Cypsela* of Mirbel and Lindley, to whom I am chiefly indebted for the synonyms of the fruits given. It is derived from the Greek ἀ, privative; and χαίνειν, to open,—that is to say, a fruit which does not open. It should, therefore, not be written "Akene," as it is commonly by many writers. The forms within [ ] are those which, though commonly used, need not be kept up.

does not adhere to the seed. *Ex.* Rose, dandelion (and all other Compositæ), buttercup, buckwheat, anemone. The seed-like bodies placed on the top of the succulent receptacle of the strawberry are also fruits of this nature.

[The term **Utricle** (utriculus), used by Gärtner, differs only from achene by the fact that the pericarp surrounds the seed loosely, like a bladder, as in the Chenopodiaceæ (or goose-foot order), &c. It is now being dropped by the best descriptive writers.]

(2.) **Caryopsis.**[1]—In this fruit the pericarp adheres to the seed. The fruits of the genus *Sporbolus*, indeed, differ only from achenes in this solitary respect. *Ex.* All grasses, including wheat, "grains," and other cereals.

(3.) **Carcerule.**[2]—It may be defined as "a many-celled fruit, in which the cells are dry, indehiscent, few-seeded, cohering by a common style round a common axis." Examples are afforded by the borage, lime or linden, Indian cress, mallow, &c., the fruits of which ultimately separate, but do not open.

(4.) **Glans.**[3]—The pericarp is hard or tough, but free from the seed. *Ex.* Acorn of oaks, chestnut, hazel (fig. 153).

(5.) **Samara.**[4]—This is a two or more celled fruit, from a superior ovary. Seeds few, indehiscent, dry, and expanded into wing-like extensions at either side. *Ex.* Elm, ash, maple.

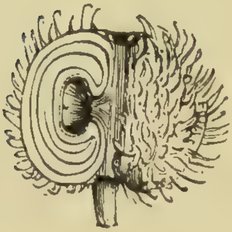


Fig. 319. — Fruit of *Galium Aparine* L. One of the achenes is cut longitudinally to show the structure of the seed. The fruit is unopened, so that the characteristics of the so-called "cremocarp" are not seen.

[**Cremocarp** [5] is the kind of fruit we see in the hemlock order (Umbelliferæ), in *Aralia, Galium* (bed-straw), &c., and is applied to a fruit, from an inferior ovary, in which the lobes separate from below, and for a time hang from the extremity of the common forked axis, or "carpophore." De Candolle calls the halves of the cremocarp, *mericarps.* They are indehiscent (figs. 288, 319).]

(6.) **Nut** proper is a hard one-celled and one-seeded indehiscent fruit, like an achene. Originally, it has one or more loculi, but they all disappear during the progress of growth.

II. (7.) **Follicle** is a fruit composed of one carpel, of which the

---

[1] *Cerio* (Mirbel).

[2] *Carcerulus; Dieresilis* (Mirbel), *Cœnobio* (Mirbel), *Synochorion* (Mirbel) *Sterigmum* (Desv.), *Microbasis* (Desv.), *Polexostylus* (Mirbel), *Sarcobasis* (DC.), *Baccaularius* (Desv.)

[3] Anglicised *gland;* but the Latin term ought to be used, to avoid confusion with the secreting organs of that name (p. 65): *Calybis* (Mirbel), *Nucula* (Desv.)

[4] *Pteridium* (Mirbel), *Pterodium* (Desv.)

[5] *Cremocarpium* (Mirbel), *Polakenium* or *Pentakenium* (Richard), *Carpadelium* (Desv.)

pericarp is usually thin, and opens by the ventral or inner side, and which thus forms a single valve, of which the two borders carry each a series of seeds. In fig. 320 A, is shown the fruit of the peony, or "hundred-leaved rose," made up of three follicles; and in fig. 320 B, a transverse section of one of the three fruits just before dehiscence. Other examples are afforded by all the members of the order Ranunculaceæ which belong to the tribe *Pæonia*, all the Hellebores, *Aquilegia*, *Caltha*, *Magnolia*, Asclepiadaceæ, Apocynaceæ.

Fig. 320.—*Pæonia officinalis*, L. A, The three follicles produced in one flower (½ nat. size). B, One of these fruits cut transversely to show the suture (*a*) by which it opens, with the seeds in position (nat. size.)

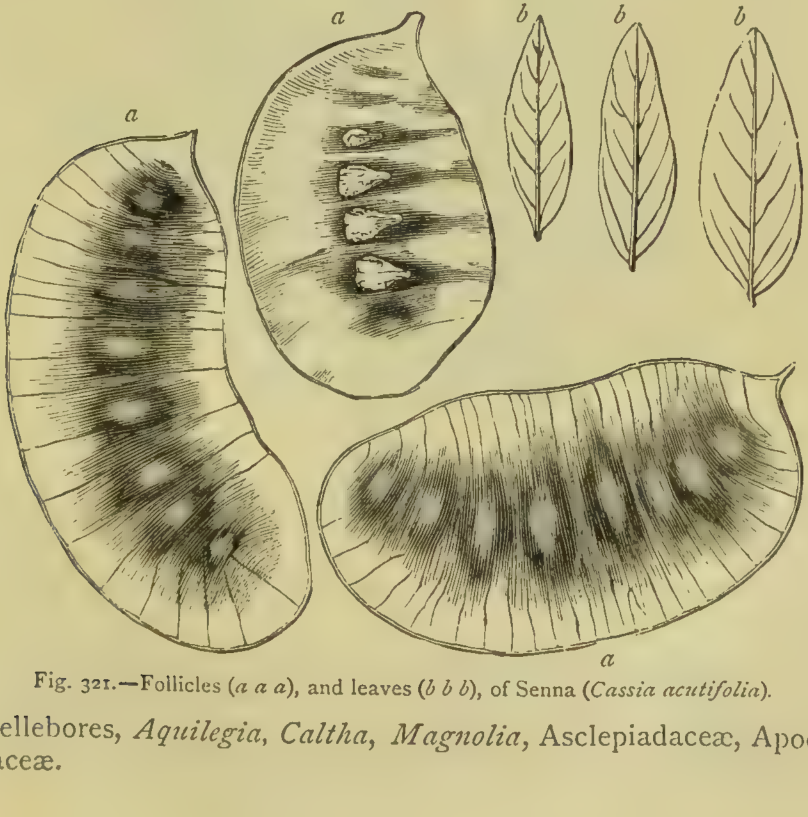


Fig. 321.—Follicles (*a a a*), and leaves (*b b b*), of Senna (*Cassia acutifolia*).

(8.) **Legume.**[1]—One-celled, one or many seeded, but differs from the follicle in dehiscing by two sutures (the dorsal and the ventral) into two pieces. *Ex.* All the order Leguminosæ, such as beans, peas, clover, &c. (fig. 322).

Fig. 322.—Tamarind (*Tamarindus Indica*). Flowering branch (*a*), and fruit (*b*). The pulp, which constitutes the internal layer of the pod and surrounds the seeds, is sweetly acidulous.

In *Astragalus*, two spurious loculaments are formed by means of a false dissepiment from either the dorsal or ventral suture; and

---

[1] Legumen (Linnæus); *Gousse* of the French botanists. For figures of different forms, the student is referred to Ralph's Icones Carpologicæ, Part I.

in *Cassia*, a number of transverse diaphragms are formed by projections of the placenta. In *Cassia Fistula*, *Cathartocarpus*, &c., the legume is indehiscent; but in such a case the line of dehiscence is indicated by the sutures. When the two sutures separate from the valves they form a kind of frame called the *replum*, as in *Carmichælia*, Lindl. It is also seen in the fruits of Cruciferæ, where it is formed by the placenta.

[**Lomentum** is a form of legume which opens transversely, breaking up into one or more one-seeded joints, which usually remain closed (as in *Desmodium*), though in *Mimosa* they split up into two valves. Usually these pieces, into which the lomentum breaks, are formed by the spaces between the seeds contracting. Sometimes spurious dissepiments form, so as to divide the fruit into many articulations or divisions (fig. 323).]

Fig. 323.—Plant which chiefly yields the gum-arabic (*Mimosa Arabica*); flowering branch (*a*), and fruit (*b*). The leaves are bipinnate.

(9.) **Siliqua** is the term applied to a slender two-valved capsule with two parietal placenta, from which the valves separate in dehiscence. *Ex.* All the order Cruciferæ, or turnip order (fig. 324). The term *Silicula* is commonly used to describe the shorter form of Siliqua, which is seen in (for example) the shepherd's-purse (*Capsella Bursa-pastoris*), *Thlapsi*, *Lepidum*, &c.; but the term is unnecessary, and might be abolished with great advantage.

(10.) **Capsule**, a fruit opening by pores, teeth, or valves—indeed the term is applied to almost any pod or dehiscent fruit of a compound pistil. *Ex.* Tulip (fig. 316), poppy (fig. 325), iris (fig.

Fig. 324. — Siliqua of *Moricandia arvensis*, (DC.) A, Entire. B, Ripe and dehiscing: *v v* The two valves; *cl* The partition (replum) to which the seeds are attached (nat. size).

Fig. 325.—Different forms of the capsules of the same species of poppy (*Papaver somniferum*), from which a large portion of the opium of commerce is made. *a* Seeds nat. size; *b* Magnified.

Fig. 326.—*Balsamodendron Myrrha* (tree producing Myrrh). 1, Fruiting branch of the natural size; 2, Capsule, unilocular and monospermous (by abortion); 3, Transverse section of the capsule and seed; 4, Seed, exendospermous, consisting of an embryo with foliaceous cotyledons; 5, Male flower (magnified); 6, Section (magnified) of the male flower (the ovary is present in an abortive condition); 7, Pollen-grain (magnified); 8, Female flower (the stamens are present in an abortive condition); 9, Section of ovary with two carpels and two bi-ovular loculaments.

251), *Lychnis*, *Viola*, *Rhododendron*, *Campanula*, rape, &c., as well as in *Balsamodendron*, the details of the anatomy of which plant are given in fig. 326.

[**Regma** is a term sometimes used to describe a fruit "in which the seeds escape by ruptures along the inner angles of the lobes, into which the fruit separates." Ex. *Geranium*, *Euphorbia*, &c.]

[**Conceptaclum** and **Tryma** are two other terms which might safely be disused. The first has been applied to the fruit of the Asclepias, Echites, &c.; and the latter to that of the walnut (fig. 279), and sometimes to the *Euphorbia* also, though it is almost impossible to define it. We have seen, however, that follicle is a fruit wide enough in its definition to embrace the first, and Regma, if necessary, to be used for the latter. The walnut is really a drupe. *Dichisma*, also proposed to be applied to the fruit of *Platystemon*, comes under the same category.]

(11.) **Pyxis**[1] is a well-marked form, in which the fruit dehisces by a transverse incision, so that when the fruit is ripe, "the seeds and their placenta appear as if seated in a cup covered with a lid" (fig. 317). Lindley looks upon this fruit as one-celled by the obliteration of the dissepiments of several carpels, from the fact that the bundles of vessels pass from the style through the pericarp down into the receptacle.


Fig. 327.—*Anamirta cocculus*—the Cocculus indicus plant.

III. (12.) **Drupe** is applied to a fruit made up of one or more carpels, the endocarp of which is cartilaginous or bony, constituting the "stone" or putamen in the last case, and free from the receptacle. *Ex.* The cherry, plum, and "stone-fruits" generally (figs. 312, 313, 327). [In *Cocos*, *Grewia*, &c., the term *false drupe* has been applied to the fruit.]

---

[1] *Pyxidium* (Ehr., Rich., Mirbel), the *Capsula circumcissa* of Linnæus.

(13.) **Pome.**[1]—This is a fruit composed of one or more carpels which are cartilaginous or bony, and enclosed within and adherent to a fleshy hollow receptacle which, with the swollen lower portion of the calyx, constitutes the edible part of the fruit. *Ex.* The apple, *Cotoneaster*, haw of the hawthorn, &c. (fig. 309.)

[The term *Sphacerocarpium* is sometimes applied to the fruit of *Hippophäe* (the sea-buckthorn, yew, &c.)]

IV. (14.) **Bacca**, or berry proper.[2] This is a fruit with one or more loculaments, generally many-seeded, indehiscent, pulpy. The attachment of the seeds to the placenta is lost at maturity, and they are scattered in the substance of the pulp. *Ex.* Gooseberry, and all the genus Ribes (fig. 252), *Vaccinum*, the fruit of the vine (fig. 278). The term is applied rather vaguely, however. Thus, the fruit of the white water-lily (fig. 328) is called a berry, though the pericarp is membranous, and is surrounded by an enlargement of the receptacle, which becomes fleshy, and bears marks of its origin in the cicatrices which are on the outside of the pericarp, marking the places where the parts of the floral envelopes were attached before they fell. The bacca is also shown (fig. 329) in the fruit of the papaw, which may be classed under this head, as well as the somewhat peculiar fruit of the duckweed (fig. 330).

Fig. 328.—*Nymphæa alba*, L. *a* Flowering plant entire, showing flowers, expanded leaves, and others in involute vernation; *b* Fruit with scars on the outside, formed by the expansion of the receptacle over the true pericarp, showing places of attachment of the perianth, which has fallen; *c* Transverse section of the fruit (p. 357); *d* Seed cut longitudinally; *e* Seed showing embryo; *f* Seed natural size and magnified.

[The term **Uva**, proposed to be applied to the fruit of the *vine*, *Solanum*, &c., in which the outer pericarp is very thin, is quite unnecessary.]

---

[1] *Melonidium* (Richard), *Pyridium* (Mirbel), *Pyrenarium* (Desvaux), &c.

[2] *Acrosarcum* (Desv.)

(15.) **Hesperidium**[1] is the term applied to the fruit of the orange, and the genus *Citrus* generally, in which the pericarp (the rind) is leathery, owing to the thickening of the mesocarp; while the endocarp, which is membranous, forms several loculaments filled with pulp, in the midst of which are the seeds, and separable one from another without tearing (fig. 330).

Fig. 329.—The Papaw (*Carica Papaya*), the type of the order Papayaceæ. 1, Whole plant; 2, Young plant; 3, Flowering branch magnified; 4, Flower-buds; 5, Baccate fruit, cut open to show seeds loose in the pulp. The fruit, when ripe, is edible; but the juice of it, when unripe, acts as a vermifuge. In some countries the leaves are used as soap.

(16.) **Pepo.**[2]—When speaking of the peculiar ovary of the melons, gourds, cucumbers, &c. (p. 357), we described this form of berry, when we adopted the theory of Lindley in reference to its production. It is "one-celled, many-seeded, inferior, indehiscent, fleshy;

---

[1] "*Hesperus*, and his daughters three,
That sing about the golden tree."
—MILTON'S "Comus."

[2] Of Linnæus—Peponida (Richards).

the seeds attached to parietal pulpy placentæ. The fruit has its cavity frequently filled at maturity with pulp, in which the seeds are embedded; their point of attachment is, however, never lost. The cavity is also occasionally divided by folds of the placenta into spurious cells, which has given rise to the belief that in *Pepo macrocarpus* there is a central cell, which is not only untrue, but impossible."

Fig. 330.—Longitudinal section of the fruit (much magnified) of a Duckweed (*Lemna gibba*).

[**Balausta**.—De Candolle designates the fruit of the pomegranate under this name. It is many-celled, many-seeded, inferior, indehiscent; the seeds with a pulpy coat, and distinctly attached to their placentæ. The pericarp, called by Ruellius the *Malicorium*, has a coriaceous mesocarp. The term **Amphisarca**, applied to the fruit of *Adansonia*, *Passiflora*, *Crescentia*, &c., in which the ovary is superior, and the outer part of the pericarp firm, leathery, or hard, may be also dropped.]

Fig. 331.—Flowering branch (*a*), fruit (*Hesperidium*) *b c*, of an Orange (*Citrus vulgaris*, var. *Bigaradia*); *d* Flower complete; *e* Pistil; *f* Transverse section of ovary.

Hitherto we have only been speaking of *Monothalmic* fruits, or the products of a single ovary. There are, however, others which must also receive a place in any carpological arrangement, and which bear the same relation to the monothalmic fruits as the inflorescence does to the flower. Such fruits may therefore be described under the head of the *Infructescence* (St Pierre), and are multiple or *Polythalmic* fruits. The following may be enumerated :—

Fig. 332.—*Humulus lupulus*—the common Hop. The upper is the male plant and flower; the lower is the female flower.

(17.) **Strobilus**, or Cone.[1]—This is applied to the fruits of firs, pines, &c., in which the naked seeds are not enclosed in a pericarp, but are placed behind woody scales, which often adhere in a firm mass (figs. 124, 125). In the hop (fig. 332) the fruits are in a kind of foliaceous cone, the scales covering them being charged with resin, that gives the active properties to the hops.

[The term **Glabulus** has been applied to the "berry" of the juniper, cone of the cypress, &c., but it does not differ from the cone proper, except in being round and having the heads of the scales much enlarged.]

(18.) **Sorosis** is the term applied to the fruit of the mulberry, pine-apple (fig. 311), bread-fruit (fig. 333), &c., in which the bracts are united with the floral envelopes into a fleshy mass, situated on an elongated receptacle, and thus converting a spike or raceme into a fleshy fruit.

(19.) **Syconus.**—This we have already described in discussing the structure of the inflorescence of the same nature in the fig. *Dorstenia*, &c. (p. 285, 397, 467; figs. 143, 310, 397).

[The **Cynarrhodum** of the rose and *Calycanthus*, we have already shown, is not a true fruit (p. 302), the true fruits being achenes; and the same is true of the **Æterio**[2] of carpological writers—the little seed-like fruits on the top of the receptacle while it is swollen and fleshy, as in the case of the strawberry (p. 464), or dry, as in the case of the *Ranunculus*, being achenes.]

The fruit having shed its seeds either by dehiscence or by rot-

---

[1] Arcesthide (Desvaux), Cachyrs (Fuchs), &c.

[2] Polysecus (Desvaux), Amalthea (Desvaux), Erythrostomum (Desvaux.)

ting, these seeds get scattered abroad in the various ways it is the province of Phyto-geography to take cognisance of—by birds, by the winds, by wild animals, by rivers, currents, icebergs (to a very small extent), and by man himself in his commerce, wars, and migrations—are deposited within fitting media for growth, and spring up into the future plant. It is therefore necessary, at this stage of our studies, to consider the structure and functions of the SEED.

Fig. 333.—*Artocarpus incisa*—the Bread-fruit tree. Scale, 1 inch to 40 feet. Leaf and fruit, 1 inch to a foot and a half.

CHAPTER XI.

THE SEED.

THE seed, we have seen, is the fertilised ripened ovule; and though its structure and general nature are in some respects the same as that of the ovule, yet owing to its higher development, and the changes produced in its maturation, it differs in many respects, both in its external appearance and internal anatomy, from the ovule. Let us therefore inquire into the structure of this important part of vegetation—the link, as it were, between the old plant, whose life is either for a time or altogether expiring, and the new one, the germ of which lies embedded within it. In appearance the seed is generally more or less roundish or flattened, though occasionally some very anomalously-shaped forms are seen. The ovoid-globose form is the most common, but it is sometimes angular, cylindrical, linear, helicoid (or rolled up like a snail), or like a snake curled up (*Ophiocarpon paradoxum*), &c., and marked externally with varied sculpture (fig. 334).[1] It is, when not sessile, attached to the seed's end by a stalk, which, as in the case of the ovule, bears the name of *funiculus*,[2] and through the stalk it is supplied with nutriment until it has attained its maturity. The scar which remains behind when the seed detaches itself at maturity from the funiculus is termed the *hilum*,[3] or "external umbilicus;" this mark may be either small or punctiform, or elongated, as in horse-chestnut, &c.[4] It is frequently black in colour. The


Fig. 334.—Seed of *Antirrhinum majus*, L., much magnified.

---

[1] These markings are sometimes of considerable use in furnishing characters for species. For an elaborate account of the sculpture of seeds see Joh. Lange, "Bemærkninger om fröenes form og skulptur hos beslægtede arter i forskellige slægter," in the Botanisk Tidsskrift (of the Botanical Society of Copenhagen), Bd. iv. (1871).

[2] Podosperm of Richard; the *cordon ombilical* of some French writers.

[3] Or hilus.

[4] Such an elongated hilum, occupying often a third of the surface of the seed, has been styled a *nauca* by Gärtner; while the brownish punctiform or point-like hilum of grasses has been called a *spilus* by Richard. Again, Turpin has called the centre of the hilum, through which the nourishing vessels pass into the

place of this hilum on the seed is generally considered the base, and the point diametrically opposite the summit of the seed. The micropyle is now closed, but the place where it existed on the ovule can be seen in most seeds. The *chalaza* and *raphe*, when present, are in most cases apparent in the seed as well as in the ovule, and the same names are applied to the seed and its relation as we have already been familiar with in the ovule. The terms *anatropal*, *campylotropal*, *orthotropal*, &c., are also equally used to characterise the relative positions of the micropyle (or corresponding position), and the place where the funiculus joins the seed, as in the ovule.

The *face* of a seed is that side which is most nearly parallel with the axis of a compound fruit, or the ventral section or sutural line of a simple fruit; while the *back* is the opposite side. The *edge* of the seed is the point of junction of the face and back. These points are best seen in a *compressed* seed (*e. g.*, lentil)—*i. e.*, flattened lengthways; when it is flattened vertically, it is said to be *depressed* (*e. g.*, nux-vomica). This distinction is of some importance. M. L. C. Richard—perhaps the best authority on the seed[1] —attaches some importance to the relative direction of the seed to the axis of the pericarp when the seeds are in determinate numbers,—these points affording good characters for the co-ordination of plants. Thus all the Compositæ have their seeds *erect*—*i. e.*, fixed by their extremities to the bottom of the pericarp or of one of its loculaments, when it is multilocular. On the contrary, it is *inverse* when it is attached in the same manner to the summit of a loculament of the pericarp, as in the Dipsacaceæ. In these two cases the placenta occupies the base or the summit of the loculament. If, the placenta being axillary or parietal, the seed directs its apex (or the part diametrically opposite to its point of attachment) towards the upper part of the loculament, it is called *ascending* (apple, pear, &c.) On the contrary, it is styled *suspended* when its summit is towards the base of the loculament (Jasminaceæ, some Apocynaceæ, &c.) The name *peritropous* is given to the seed when its rational axis (*i. e.*, the line which would pass from its base to its summit) is transverse in relation to the walls of the pericarp. When the seed is attached by a funiculus, if that is long and thin, it may exercise a great influence on the true direction of the seed. Thus, for example, in *Thesium*, *Statice*, and in a certain number of *Rutaceæ*, the seed is *inverse*, and hangs from

---

seed, the *omphalodium*. These superfluous names, luckily adopted by few any descriptive botanists or teachers, are specimens of the absurd extent to which the multiplication of terms has been carried in all departments of organography, but more particularly in that relating to the fruit and seed.

[1] Observations on the Structure of Fruits and Seeds, translated by John Lindley (1809).

the summit of an erect funiculus attached to the bottom, or near to the bottom, of the loculament. The position of the seed in the pericarp has no reference to the direction in which the fruit hangs (pendulous, erect, &c.); and indeed the two may be quite in opposition—*i. e.*, the seed may be pendulous while the fruit is erect.

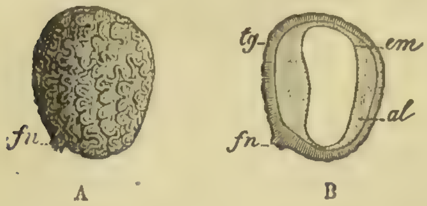


Fig. 335.—Seed of Tobacco (*Nicotiana Tabacum*, L.) A, Entire; *fn* Part of funiculus. B, Longitudinal section: *fn* Extremity of funiculus; *tg* Hard thickened tegmen; *al* Endosperm; *em* Embryo (mag. 20).

STRUCTURE OF THE SEED.

Integuments.—The seed, like the ovule, consists of a nucleus or kernel enclosed with two coats or integuments—viz., the *Spermoderm* and the *Tegmen*—in general readily separating from one another.

1. The *Spermoderm*,[1] or outer coat, is formed by the blending of the primine and secundine, which in most seeds are soldered together, but in some cases (the seed of the castor-oil plant, for example) they are perfectly distinct. In this case the secundine is termed by De Candolle the *mesosperm*,[2] *sarcoderm*,[3] or *sarcosperm*, and, according to him, serves in the seed the same purpose as the mesocarp in the fruit. Such seeds are usually thickly swollen with juices, and have accordingly been called *semina baccata*. In anatomical structure the spermoderm presents great diversity in the number and nature of the layers of cells which compose it, and may be with or without bundles of vessels intermixed. In colour it differs much, as it also does in the form and nature of its inequalities and physical composition. It may be coriaceous, crustaceous, spongy, bony, fleshy, woody, or simply membranous, smooth or rough, polished with appendages (figs. 334, 335).

2. The *Tegmen*,[4] or inner coat, is much thinner than the outer one just described, though in some exceptional cases it is thickened (fig. 335). It may even be entirely wanting.

The thickness of the integuments varies much in different genera. Thus, in the glands of the oak, the seeds of the beech, wal-

---

[1] Of De Candolle, from σπὲρμα, seed; and δέρμα, covering: also called by Richard the perisperm (περι, around; and σπὲρμα), and afterwards the *episperm* (ἐπὶ, upon; and σπὲρμα) or *testa*, DC. (Latin for a shell); lorique (*lorica*) of Mirbel; *tunica externa* of Willdenow.

[2] μὲσος, middle; and σπὲρμα.

[3] σὰρξ, flesh; and δέρμα.

[4] Of Mirbel; *Endopleura* (endoplévre) of DC. (ἔνδον, within; and πλευρά, side); the *tunica interior* of Gärtner; *tunica interna* of Willdenow: also called *hilofère* by Mirbel.

nut, hazel, almond, cherry, prune, and other Amygdalaceæ, these are dry and membranous, and the inner coat immediately surrounds the embryo. But in the fruits of the *Opuntia Ficus-Indica* (Indian fig), the numerous seeds with the fleshy integuments constitute the sugary and acidulous portion of the fruit, as is also the case in the passion-flowers and pomegranate. In these last-named plants the pericarp is even hard and woody. In the yew, ginko, peonia, magnolia, and cycas, the integuments are formed of several layers of cells, and the internal layer forms a firm nut, so that the fruits of such plants might be mistaken for true drupes—so much the more that the endosperm is surrounded by a tolerably consistent yellow envelope.[1]

M. Béchamp has announced the discovery, in the fleshy integument of the ginko (*Salisburia adiantifolia*, one of the yew order), of a series of acids, chief among which are formic, caproic, besides proprionic and valeric or phocenic acids. In the flax, and some other plants, the integuments of the seed develop a mucilage.

On the whole, according to Schleiden, the integuments of the ovule experience so many changes during the process of ripening, that their original number cannot be often made out in the seed. "They are sometimes all consolidated so as to form but one; or they are broken up into many layers, having no relation to the original numbers of integuments. In *Menyanthes* (the bog-bean), which has but one integument of the ovule, the seed appears to have two, because of the separation and lignification of the epidermis of that integument; and in *Canna* there are five layers of tissue resembling integuments, though the ovule has not even a complete integument. In the case of spurge-worts, rock-roses (Cistaceæ), and daphnads, a peculiar process takes place—namely, upon the seed becoming ripe the external integument is gradually absorbed, until nothing but a thin membrane is left, usually described as an *epidermis testæ;* or, as in spurge-worts (Euphorbiaceæ), it has been described as an aril (p. 501);[2] and, on the other hand, the actual modified epidermis testæ has also been described as an aril—for instance, in the oxalids."

In some plants (*e.g.*, convolvulus) the integuments are thrown off separately during germination.

Appendages of the Integuments.—Exterior and secondary to the seed are various parts which may be described as appendages to the integuments; these are wings, hairs, &c., and the peculiar appendages known as the arillus, caruncle, and strophiole.

Hairs.—These are found on various seeds, but the most inter-

---

[1] Charles Martins in Richard, lib. cit., 286.

[2] See Baillon, Etude générale du groupe des Euphorbiacées, for discussion of this and similar points.

esting ones are those of the cotton (*Gossypium*), one of the Mallow order (Malvaceæ), which constitutes the textile material known as "cotton." Each thread of cotton consists of a single cylindrical cell, often of considerable length, which, when dried, twists upon itself in a sort of spiral manner, very characteristic of this material (p. 40, fig. 336).

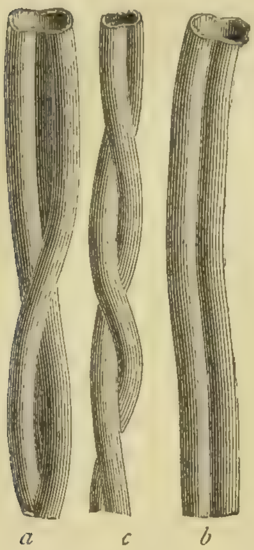


Fig. 336.—Hairs of Cotton (*Gossypium herbaceum*), with the characteristic twist which they take in drying. *a* Tubular hair beginning to flatten on the median line; *b* The same hair more flattened and twisting on itself; *c* As it appears when completely dry. The figures represent the hairs as rather too rounded. After being dried, they are merely flattened bands with rounded margins (mag. 400 diameters).

The internal wall of the pericarp of Bombaceæ also develops the superficial cells into long woody or cottony hairs, which form a material analogous in aspect to cotton, but which cannot be utilised in the same manner. According to M. Duchartre, it is the columella in the genera *Eriodendron*, *Bombax*, and *Salmalia*, which is charged with the production of these hairs, while it covers the interior of the valves themselves in *Ochroma Lagopus*, Sw.

In various species of Epilobium and Asclepiadaceæ, the seeds are furnished with a tuft of hairs called a *coma*, or aigrette, attached to one end, in the case of the Asclepiadaceæ at the summit, but in that of the Epilobium at the end near the chalaza; while in the case of several Bromeliaceæ the entire seed is surrounded by a sort of wing hairs. This *coma* has, however, the student must remember, no analogy whatever with the tuft (pappus) found on the achenes of the Compositæ — since, the one being found on the entire fruit, and those mentioned above on the seed alone, there can be no connection one with the other.

Dr Asa Gray has called attention to the fact that the integument of "numerous small seeds is furnished with a coating of small hairs containing spiral threads, and usually appressed, and confined to the surface by a fibre of mucilage. When the seed is moistened the mucilage softens, and these hairs spread in every direction. They are often ruptured, and the extremely attenuated elastic threads they contain uncoil and are protruded in the greatest abundance, and to a very considerable length. This minute mechanism subserves an important purpose in fixing these small seeds to the moist soil upon which they lodge when dispersed by the wind. Under the microscope, these threads may be observed on the seeds of most Polemoniaceous plants,[1] and on the achenes of Labiate[2] and Composite plants—as, for example, in many species of *Senecio* or groundsel."

---

[1] *E.g.*, *Collomia linearis.*

[2] *E.g.*, *Salvia.*

This may be something of the same nature as the layer of spiral vessels which have been described as existing below the epidermis of *Casuarina*, *Swietenia febrifuga*, &c. In most Bignoniaceæ, and in many other plants, the cellular tissue of the integuments of the seed is reticulated.

Wings.—These expansions of the spermoderm are seen in the catalpha, trumpet-creeper (*Tecoma radicans*), &c.; but the "winged seed" of the firs and pines is in reality only "a part of the surface of the scale or carpel to which it is attached, and which separates with it."

The Arillus.—This is an exterior covering with which some seeds are provided, usually incomplete and of a fleshy texture, entirely exterior to the other integuments, and arising from the expansion of the apex of the funiculus, or, if this is not manifestly present, from the placenta itself. It forms, in fact, an accessory integument to those seeds in which it is formed. M. J. E. Planchon[1] has distinguished a *false arillus* or *arillode* (arillodium), reserving the first name for the true arillus arising from an expansion of the funiculus, and the latter for those which arise from the border of the exostome—the one growing from the funiculus to the micropyle (that is, from below upwards), the other from the micropyle to the funiculus (or in an exactly opposite direction—viz., from above downward). It is not, however, always easy to distinguish the two, unless the development of the seed is followed; for neither arillus nor arillode is found in the ovule, but forms during the development of the seed. However, owing to their mode of development, the arillus—according to Brown's observations—when present, always covers up the micropyle, while the arillode leaves it uncovered. This test forms an easy method of distinguishing the two when a more analytical method is not practicable.

As examples of the *arillus*, we may cite the seeds of the passion-flower when it forms a loose fleshy sack with a large opening at the extremity. In the order *Dilleniaceæ* we find every extent of development of the arillus—from *Pachynema* and *Hemistemma*, in which it forms a simple cup, surrounding the lower part of the seed, to *Tetracera*, where it almost entirely covers it. In the seeds of the white water-lily (*Nymphæa*) it forms a thin, semi-transparent, cellular bag, open at one end; in *Turnera* it appears as a

---

[1] Mémoire sur les développements et les caractères des vrais et faux arilles, &c., Montpellier, 1844; Comptes rendus, Dec. 1844; Ann. des Sc. Nat., 3e sér., 1845, iii. 275-312. Pages 33-53 of vol. ii. of Lindley's Introd. to Botany contain almost a full translation of this able essay. The characteristic sneer with which the illustrious author of the 'Grundzüge der Botanik' greets M. Planchon's labours, only shows how incapable he is of rightly valuing the labours of his contemporaries or adversaries—a fact of importance to keep in mind when reading his works.

mere lateral scale (Gray); while in Bixia, *Cytinus Hypocistis*, and various genera of Sapindaceæ, it forms a more or less extensive appendage to the seeds.

The *false arillus*, on the other hand, is seen in the spindle-tree genus (*Euonymus*); and the similar pulpy envelope of the seeds of *Podophyllum* and *Celastrus*, and other genera, is probably of the same nature. It is also seen on the seeds of *Polygala*,[1] and various other plants; but the one on which it is most familiarly known is on the common nutmeg (*Myristica fragrans*), where it forms an irregular network of a fleshy character, orange-red in colour, and highly scented, known in commerce under the name of mace (fig. 337).

Caruncle (Caruncula).—This is very analogous to the false arillode. It consists of the thickened edge of the exostome, in the form of a fleshy, lenticular, or hemispherical excrescence, at the side of the hilum. Examples are seen in *Ricinus*, *Euphorbia*, and many other Euphorbiaceæ.

Fig. 337.—Seed of Nutmeg (*Myristica fragrans*), with the arillode which constitutes the spice called "Mace."

Strophiole.—Under the name of Strophiolæ,[2] Gärtner described certain cellular excrescences on the integument of various seeds (*e.g.*, *Chelidonium majus*, *Dicentra*, *Sanguinaria Canadensis*, or blood-root of America, &c.), formed independently of the funiculus or exostome, and, for the most part, placed on the raphe, where they form a conspicuous crest along one side of the seed.[3]

Nucleus.[4]—The nucleus or kernel of the seed comprises all those parts covered by the integuments, and may consist of the *endosperm* and *embryo*, or of the embryo alone. The kernel is attached to the integuments by the chalaza, though in the ripe seed this connection is usually destroyed. The embryo must always be present in every perfectly fertilised seed, and, as in the case of *Phaseolus*, it may form the only part of the kernel. At other times there is, in addition, a distinct body called the endosperm present (as in the castor-oil seed, *Oxalis*, snapdragon, to-

---

[1] The distinction between the different organs of the aril nature is so little defined that by some authors this is called a caruncle, while Schleiden declares it is only a "rather loose epidermis to the seed."

[2] Sometimes called *cristæ* or crests, from their appearance.

[3] The term *embryotega* has been given by Gärtner to a small callosity near the hilum of some seeds (*e.g.*, the bean), which at the period of germination is pushed up like a lid to allow of the emission of the radicle.

[4] *Amande* of the French, and *Samenkern* of the German botanists.

bacco, &c.) The embryo grows into a new individual; but the endosperm, if present, is consumed in supplying nourishment to the embryo in process of growth.

Endosperm or Albumen.—This part of the kernel is thus not essential to the life of the seed, not being present in those of all species of plants. The embryo, we have seen (p. 414), is formed in the embryonic vesicle, which shows itself in the upper part of the embryo sac, and in most cases the endosperm originates from a tissue formed within the embryo-sac. Robert Brown has, however, shown that in Nymphæa and other Nymphæaceæ, Zingiberaceæ, Piperaceæ, Cabombaceæ, Saururus (Saururaceæ), a cellular tissue develops exterior to the embryo-sac, so as to form two endosperms, the one surrounding the other in a concentric form. In some cases the cellular tissue, forming the bulk of the kernel, is absorbed by the embryo in developing, and in this case there is no endosperm present in the adult seed, the embryo forming the sole constituent of the kernel; but in other cases, on the contrary, the cellular tissue constituting the walls of the kernel (and the second one formed outside the embryo-sac, if present) remain and increase, and take a fleshy or horny consistence, forming round the embryo the cellular substance known as the endosperm or albumen[1] (fig. 338).

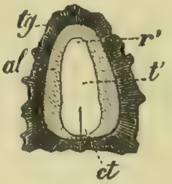


Fig. 338.—Longitudinal section of seed of Snapdragon (*Antirrhinum majus*, L.), greatly magnified. *tg* Integuments; *al* Endosperm; *t'* Caulicle; *r'* Radicle; *ct* Cotyledons of the embryo.

---

[1] The latter term, the one most commonly applied to it, originated with Grew (and in more recent times was revived by Gärtner), under the idea that it had some analogy with the albumen or white of the egg. The term ought, however, to be dropped, as it is apt to be confounded with the proteine substance of that name. I have therefore preferred to use Richard's term of endosperm (ἔνδον, within; and σπέρμα, seed). A. L. de Jussieu has called it the *perisperm*; while other authors, following the lead of Schleiden and Vogel, have proposed to restrict the name of endosperm to the substance as formed within the embryo, and to apply that of perisperm to that which develops in the walls of the kernel. Still, independently of the fact that it is confusing to apply to the endosperm names which have been long used in a totally different signification, this nomenclature, though perhaps useful as being more precise than any other, is apt to lose its utility in the fact that it aims at a precision which in practice cannot be kept up; for in ripe seeds it is almost impossible to point out the distinction between the two endosperms, this only being able to be done by tracing the development of the seed. Others have attempted to simplify the matter by giving the term *vitellus* to the inner endosperm, while the name *albumen* is reserved for the outer one, the simile of the yolk and white of the egg being still followed. This, however, only makes "confusion worse confounded." Finally, it may be worth remembering that it is the *medulla seminis* of Jungius, and the *secundina interna* of Malpighi. Perhaps the nomenclature given in the text may simplify the matter.

Finally, Schleiden and Vogel[1] have announced that in the genus *Canna* there exists another kind of endosperm, which has its origin neither in the embryo-sac, as in the great majority of cases, nor in the kernel, but is well developed in the thickness of the tissue in the region of the chalaza. There are therefore three ways in which the endosperm originates—viz.:

(1.) By the development of the tissue forming the walls of the kernel, or *nuclear endosperm.*

(2.) From the cellular tissue which is produced within the embryo-sac, or *embryonic endosperm.*

(3.) From that produced in the region of the chalaza, or *chalazian endosperm.*

Variations of Composition of the Endosperm.—The endosperm is a cellular tissue without vessels; but owing to the fact of its being moulded on the cavity into which it is gradually introduced, it is extremely smooth or sinuous, according to the smoothness or sinuosity of the walls of that cavity. It is usually white,[2] and composed of vegetable jelly, and insipid to the taste. In some cases, again, it shows, when cut into, a wrinkled or variegated appearance. An example of this is afforded by the seeds of the so-called "papaw" of North America (*Asimina triloba*), and all the rest of the Anonaceæ, or custard-apple family, to which it belongs, and still more familiarly in the betel-nut, nutmeg, and seed of the ivy. These sinuosities, different in colour and consistence from the rest of the endosperm, are probably caused by inflections of the tegmen during the progress of growth. Such endosperms are termed *ruminated.*

The endosperm is also not of the same consistency in all seeds:

(1.) It may be *farinaceous* or mealy—*i. e.*, with the cellular tissue filled with starch-grains, as in wheat and other "farinaceous Graminaceæ," in which it is accompanied by gluten.

(2.) *Oily*, when a fixed oil is mixed with it, as in the cases of poppies, *Ricinus*, and cocoa (*Theobroma*).

(3.) *Fleshy*, when the cellular tissue has thick walls, and contains juices of various kinds, as in the berberry, cocoa-nut, *Ricinus*, various Euphorbiaceæ, &c. From fleshy seeds they are all gradations to

(4.) *Corneous* or horny, as in the case of the coffee-bean, date-palm, and *Phytelephos macrocarpa*, the endosperm of the latter of which consists of a hard white body, known in the arts as "vegetable ivory;" and

(5.) It may be *mucilaginous*, when the bulk of it consists of mucilage or vegetable jelly, as in the Morning glory and Mallows.

---

[1] Ueber das Albumen, insbesondere der Leguminosen; Nova. Acta Acad. Nat. Cur., Bd. xix. heft ii. ss. 54-95.

[2] In the mistletoe it is *green.*

Presence or Absence of the Endosperm.—With the exception of the orchids and a few other species, it is rarely that the endosperm is not present in some stage of the seed, showing that it must serve some important purpose in the nutrition of the embryo in its very earliest period. In many orders it is, however, entirely wanting in the adult state of the seed, having probably been absorbed or transformed in an earlier period of the seed-life. The Cupuliferæ, Fraxinaceæ, Ulmaceæ, Cruciferæ, Rosaceæ, &c., are examples of orders the seeds of which want endosperm in their adult state, and are therefore styled *exendospermic* or *exalbuminous*;[1] while those which, on the contrary, possess endosperm (such as Coniferæ, Cycadaceæ, Euphorbiaceæ, snapdragon family, Gramineæ, &c.), are termed *endospermic* or *albuminous*.[2]

Variations of the Endosperm.—Even when the endosperm is present, M. Duchartre and other observers have pointed out that there are great variations in the amount of it present in the seeds, not only of closely-allied orders, but even of genera in the same order, and even in species belonging to the same genus. For instance, while most of the genera in the *Araceæ* are provided with a large amount of endosperm, the genera *Scindapsus* and *Pothos* want it entirely. On the contrary, in the Leguminosæ, which are usually described as wanting endosperm, Schleiden and Vogel have shown that there are so many exceptions as to almost invalidate the rule. For instance, the whole of the sub-orders *Mimoseæ*,[3] several of the genera of *Cæsalpineæ*,[4] and even some *Papilionaceæ*,[5] possess this in a greater or less degree. Finally, the most curious fact is, that while most of the species of the genus *Acacia* have endospermic seeds, *A. stricta*, *graveolens*, *melanoxylon*, *longifolia*, *lopantha*, &c., are exceptions to the rule; and several irregularities are presented by the genera *Æschynomene*, *Lathyrus*, *Ononis*, and *Lupinus*. Several other

---

[1] *Semina exendospermica* or *S. albuminosa*.

[2] *Semina endospermica* or *S. albuminosa* (*S. perispermica*, Juss.)

[3] *E.g.*, according to Schleiden and Vogel, in the greater number of the genus *Acacia*, and in *Mimosa*, *Prosopis*, *Desmanthus*, whilst it is wanting in *Inga* and *Entada*.

[4] In *Cæsalpinia*, *Hæmatoxylon*, *Poinciana*, *Tetragonolbus*, *Cassia*, *Gleditschia*, &c., and not in the generality of the others.

[5] In *Phaseolus*, *Pisum*, *Vicia*, *Orobus*, &c., there is none; but the genera *Melilotus*, *Trifolium*, *Lotus*, *Trigonella*, *Astragalus*, *Robinia*, and several others, possess a greater or less amount. It is not found in *Swartziæ* and *Geoffreyæ*. Schleiden was not, however, the first to announce the discovery of endosperm in the seeds of Leguminosæ. Gärtner, Jussieu, Guillemin, Perrottet, and others, long before his time, contended for its existence in a greater or less extent in various genera. De Candolle called it *Endopleura tumida*. In later times, Lindley made admirable investigations on the subject.

examples from other orders—and such facts are continually being recorded—might be given; but the above may suffice, as showing the variability of the presence and absence of endosperm.

Embryo.[1]—The embryo is the fleshy body in the seed which develops into the future plant. It may be either accompanied or unaccompanied by endosperm. In this last case the embryo is covered directly by the integuments. It is a perfect plant in miniature at the very first, with axes and lateral organs, an inferior portion destined to extract nutrition from the soil (the radicle), and an upper portion not so easily distinguished, and apt to be confounded with the former—viz., the plumule; while the lateral organs are the cotyledons. At the end of the plumule is a little bud called the *gemmule.* The embryo, therefore, consists of the following parts: 1, the radicle; 2, the cotyledons; 3, the plumule, consisting of (α) the caulicle or stem *in embryo,* terminated by (β) the *gemmule* or bud.[2] Before, however, describing each of these parts in succession, let us glance at a few points in connection with the embryo as a whole.

Situation of the Embryo in regard to the Endosperm, &c.—In endospermic seeds the embryo maintains different positions in the endosperm, or in relation to it. The chief of these may be stated briefly:—

(1.) The embryo may be placed in the interior of the endosperm, which covers it in every part, as in *Oxalis* (sorrel).

It is then called *interior* (intrarius, Rich.)

(2.) It may be *axile,* when it is placed in the direction of the axis of the endosperm, as in the castor-oil seed (Ricinus).

(3.) It may be *lateral* or *excentric,* when it is placed towards one side of the endosperm, as in the cocoa-nut, and in most other palms.

(4.) It may be placed, not within the endosperm, but on one part of the surface of it, as in maize, wheat, and other grasses, Polygonum, &c. In this case it is called *exterior* (extrarius, Rich.)

This position of the embryo may be caused by the unequal development of the parts of the endosperm. It is, however, worthy of remark, that while the embryo of all grasses is *exterior,* that of the neighbouring order of Cyperaceæ is interior.

(5.) The embryo may be recurved on the surface of the endosperm, which it embraces in the form of a ring, so as to be external, or nearly so. *Ex.* Goosefoot, chickweed, *Mirabilis,* and

---

[1] Also called the *Corcalum* (little heart). Sometimes also called the germen (see *Ovary,* p. 350).

[2] Saint Pierre has applied the name of *mesophyte* or *collet organique* to the point which separates the root (or descending axis) from the stem (or ascending axis).—Dict. de Botanique, p. 635.

Nyctaginaceæ. Such peripherical embryos are always found in seeds, of which a campylotropal ovule is the origin.

It may, again, be only arcuate, as in *Rubia tinctorum* (fig. 340). This may be taken as the medium curvature between axillary embryo on the one side and the peripherical on the other. There are all gradations. It may be also falcate, uncinate, *gnomonical* (bent at right angles), *sigmoid* (like the letter S), &c. In the Dodder order (Cuscutaceæ), it may be bent in the form of a spiral, like a snail's shell.

(6.) *Accumbent*, when the embryo is bent in such a manner that the radicle lies along the edge of the cotyledons. Ex. *Matthiola, Cheiranthus, Nasturtium, Arabis, Cardamine, Cochlearia*, &c.

(7.) *Incumbent*, "when the radicle rests against the back of one of the cotyledons, in the median line of one of them, or in proximity to it." *Ex.* Shepherd's-purse (*Capsella Bursa-pastoris*) *Hesperis, Sysimbrium, Lepidum, Camelina*, and fig. 341.

The last-named position of the embryo furnishes an important character for the subdivision of the order Cruciferæ. Thus, in the division *Pleurorhizæ*,[1] the cotyledons are accumbent, while in the *Notorhizæ*[2] they are incumbent. The first mode of arrangement is indicated in descriptive works by certain contractions.

Sometimes the embryo is very small compared with the mass of endosperm, and occupies but a comparatively small place in the kernel; but at other times it is much larger than the endosperm, which, in such a case, as in the Labiatæ, is so thin as to be reduced almost to a pellicle.

In most cases there is only one embryo in each seed;[3] but occasionally—in the orange and hazel-nut, and commonly in conifers, cycads, onions, and mistletoe—more than one is developed,[4] though now and then a union of these embryos takes place.[5]

Direction of the Embryo.—The *absolute* direction of the embryo is that which it affects, all the surrounding parts being left out of the question. Thus it may be, we have seen, straight, incurved, &c.; while the *relative* direction is that which it observes relatively to the seed, just as we have already noted (p. 497) the position of the seeds in reference to the pericarp. Both the relative and proper directions are determined by means of the two extremities of the seed. The absolute direction we have already considered in the preceding paragraph. Let us now consider, in a similar manner, the *relative direction* of the embryo. Almost universally the hilum is regarded as the *base of the seed*, while the point at which

---

[1] πλευρὰ, side; and ῥιξα, root.

[2] νῶτορ, back; and ῥιξα.

[3] Monembryony (μόνος, one; and embryo).

[4] Polyembryony (πολὺς, several; and embryo).

[5] I state this fact in reference to the two last-named plants on the authority of Dr Lindley, as I have never been able to meet with a case of that nature.

the radicle appears is considered as the *base of the embryo.* Relatively towards the fruit, the embryo, looking upon the radicle as the base, may be *inferior* or *descending*, when it is directed towards the attachment of the pericarp—*i. e.*, towards the base; *superior* or *ascending*, when the opposite is the case. Finally, it is *centripetal* or *centrifugal*, as the radicle is directed towards the interior or exterior of the fruit; and *vague* (vaga), or wandering, when it has no evident or uniform direction in reference to the pericarp.

(1.) In an orthotropal ovule the hilum is the antipodes of the micropyle. Accordingly, in a seed derived from such an ovule, the direction of the embryo is opposed to that of the seed—*i. e.*, "its cotyledonary extremity corresponds to the hilum." This we see in the *Thymelaceæ*, *Naiadaceæ*, *Melampyrum*, *Helianthemum*,[1] buckwheat, *Cistus*, *Urtica*, &c. Such an embryo Richard calls *anatropal*[2] or inverse.

(2.) In a seed derived from an anatropal ovule, the base of the embryo and that of the seed correspond, the extremity of the radicle being brought into the immediate vicinity of the hilum. Such a relation Richard indicates by applying the term *homotropal*,[3] or erect, to the embryo. This we see in most Leguminosæ and Solanaceæ, linden, violet, and in many Monocotyledons.[4]

(3.) In a seed derived from a campylotropal ovule, the embryo is necessarily curved upon itself, so that the two extremities also meet towards the hilum. Such an embryo is styled *amphitropal*,[5] or curved, and is seen in pinks, Cruciferæ, the common *Stellaria media*, various species of the Atriplicaceæ, mignonette (*Reseda*), &c.

(4.) The term heterotropal[6] is applied to cases in which the relation of the radicle and the micropyle are entirely different, owing to such a displacement of the radicle in the progress of growth that it becomes directly parallel to the plane of the hilum. Examples of such an arrangement can be seen in the Primulaceæ (notably in the pimpernel, *Anagallis arvensis*), in which the seed is the shape of a truncated cone.

Having once determined the position of the embryo, it is easy, as the same celebrated botanist whom we have quoted points out, to determine its direction in reference to the other chief points of the integument. For instance, the position of the point of the radicle constantly indicates that of the micropyle, these points of structure being constantly in the same relation. In a seed derived

---

[1] Eléments de Bot., ed. x., p. 290.

[2] ἀντι, against; and τροπή, the act of turning—*i.e.*, turned in a contrary direction.

[3] ὁμός, alike; and τροπή.

[4] Richard has also applied the term *orthotropal* to a perfectly rectilineal embryo, as with Compositæ, Umbelliferæ, apple, plum, &c.

[5] ἀμφι, around; and τροπή.

[6] ἕτερος, different; and τροπή.

from an orthotropal or anatropal ovule, the embryo (the radicle) is opposed to the chalaza; in a seed derived from a campylotropal ovule, the radicle approaches laterly towards the chalaza, without, however, being opposite to it, as in the other case.

These relative directions of the embryo are valuable as furnishing characters for the co-ordination of natural groups.[1]

Connection between the Endosperm and the Embryo.—Except in the Coniferæ, there is no organic connection, or even adherence, between the embryo and the endosperm. In this order, however, the radicle appears to be continuous with the endosperm, the adherence between the two being due to the remains of the suspension of several embryos, which were produced in the same ovule, but of which one alone attained its complete development (p. 414).

Let us examine more in detail the different parts of the embryo of a young plant shut up in the seed.

(1.) *Radicle.*[2]—This is one of the extremities of the embryo, and owing to its mode of origin, is always directed towards or near to the micropyle. If the embryo is straight, or only shares in the general curvature of the seed, then the radicle is directed to the opposite extremity—viz., to the chalaza. It is usually the first portion pro-

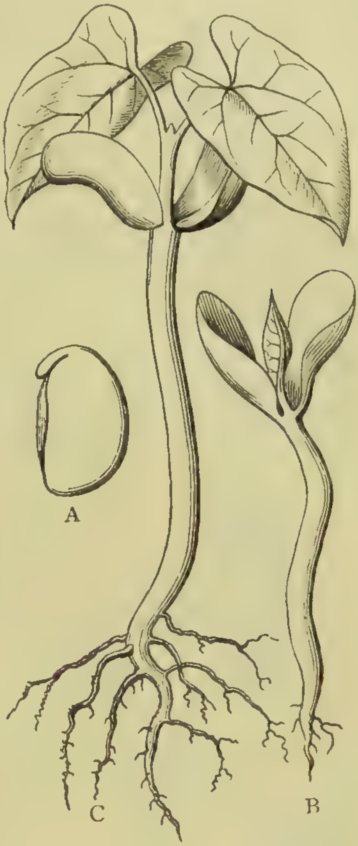


Fig. 339.—Illustrations of Dicotyledonous Germination. A, The embryo (*i. e.*, the entire kernel) of the bean. B, The same in early germination, the thick cotyledons expanding and showing the plumule. C, The same still more advanced in germination, showing the caulicle now developed into the first internode, and the gemmule expanded into a pair of leaves borne on it (after Gray).

---

[1] It would, however, be a more scientific, and an infinitely less embarrassing nomenclature, if all the terms applied to the position of the ovule were also used with reference to the seed. This may come to pass when it is thoroughly understood that to manufacture a new barbarous compound of indifferent Latin, or still more dubious Greek, *is not to discover a new fact.* However, so long as they are used, it is necessary for the student to know them; though the men least capable of advancing science, are, to use Schleiden's words, most anxious for the poor short-lived notoriety gained by coining a new word, and, I may add, of the less excusable one of using them.

[2] Radicula, Rostellum, Rhizoma.

truded through the integuments of the seed. It is the axis or rudimentary stem: from its lower portion the rootlets proceed; from its upper the gemmule; the cotyledons are also attached to the upper end. Its nature and mode of development in Monocotyledons and Dicotyledons we have already discussed while describing the root (p. 128), and will hereafter have occasion to say something more while describing the process of germination. In some cases the radicle (or rather the caulicle) is very large, while the cotyledons remain small; such embryos Richard has called *macropodous*.[1]

Fig. 340.—Longitudinal section of the seed of *Rubia tinctorum*, L. (Madder). *al* Endosperm; *ct* Cotyledons; *t'* Caulicle; *r* Radicle, or radicular extremity (mag. 5 times).

(2.) *Plumule.*—This is that part of the embryo in a line with the radicle, which, in fact, it is only a continuation of superiorly. It gives birth to the stem, and commences at the point of insertion of the cotyledons, which are attached to it. It may be divided into two parts —(*a*) *the caulicle*, terminated by (*β*) *the gemmule.*

Fig. 341. — Transverse section of the siliqua of *Moricandia arvensis*, DC., passing through a seed. In the embryo of this is the radicle *r*, directly the length of the median line of one of the two cotyledons (*ct*), which are hollowed into a groove, which are conduplicate. The section of the siliqua shows the two loculaments, and the partition which separates them (10/1). (This is an exendospermic seed.)

(*α*) *The Caulicle*[2] is not easily made out in all embryos before germination; but as soon as this process sets in, it lengthens and becomes quite distinct (fig. 339). The point between the insertion of the cotyledons into it, and the crown of leaves (gemmule) with which it is terminated, constitutes the first internode. As the name expresses, it is really the "little stem."

(*β*) *The Gemmule*[3] (fig. 339), or terminal bud of the plumule, is, like all terminal buds, composed of an axis continuous with the axis of the plumule, and of rudimentary leaves. In Dicotyledonous plants it is usually placed between the cotyledons, which by their approach cover and conceal it. In Monocotyledons it is placed in a little *fossette*, or pit, as the base of one side of the cotyledon, which pit represents the sheath of the cotyledonary leaf. The gemmule gives origin to a shoot which commences the aerial stem of the plant, and upon which grow the rudimentary leaves, which in due course take the form, position, and characters which belong to the leaves of the particular species to which the embryo may belong.[4]

[1] μακρός, large; ποῦς, ποδός, foot.

[2] Cauliculus, scapus; the *tigelle* (tigellus) of the French botanists.

[3] French; Latin *gemmula*, the diminutive of *gemma*, and means literally the "budlet."

[4] One of the most successful investigators of the physiology of the seed—M.

(3.) *Cotyledons.*[1]—These are the lateral appendages of the embryo, and may be either one or two in number. Take, for instance, a bean, and the two lobes into which it divides show the two cotyledons; while a grain of wheat is solid, and cannot be divided—in other words, it has only one cotyledon. This elementary arrangement of the seed-leaves in the young plant is important, in so far as it is accompanied by other differences in other parts of the plant which allow us to form the two great divisions of the vegetable kingdom, called respectively *Dicotyledons* and *Monocotyledons*—plants the seeds of which have two cotyledons or only one (p. 73). This character does not, however, invariably hold true. In Coniferæ (pines, firs, &c.) there are apparently from one to ten, and even fifteen (there being much variation even in the same plant) cotyledons, arranged in a verticil. Hence the accuracy of the classification named, founded on the number of cotyledons, has been called in question; and another division, founded on this supposed peculiarity in Coniferæ, has been founded by some systematists, and called *Polycotyledons*, or plants with many cotyledons. M. Duchartre has, however, shown[2] that in this order of plants there are in reality originally only two cotyledons, which are repeatedly divided, so as to form, in appearance, many cotyledons, and that therefore the old classification is in reality quite correct. Some Leguminosæ and Cruciferæ also occasionally show examples of plants with three cotyledons, or, as in the case of the cruciferous genus *Schizopetalum*, four cotyledons; but M. Duchartre, in the Memoir quoted, shows that, as in Coniferæ, there are in these plants only two cotyledons, subsequently, in the progress of development, divided into a greater number.[3] Three cotyledons have also been seen in embryo plants of *Correa*, *Cratægus*, *Dianthus sinensis*, *Daucus Carota*, *Cerasus Lauro-cerasus*, bean, a *Solanum*, *Apium Petroselinum*, marigold (*Calendula*), beech (Fagus), various Loranthaceæ (*Nuytsia*, *Psittacanthus*), &c., and in *Cola acuminata*, the cotyledons in some seeds vary from two to five.[4]

Arthur Gris—used the seeds of the castor-oil plant, as best fitted to follow out the anatomy and germination of seeds in general on. See also Chatin, Ann. des Sc. Nat. Bot., 5e sér., xix. 5.

[1] κοτυληδὼν. Mirbel admitted two parts of the embryo—viz., the cotyledons and the *blastema*, a term under which he included the radicle and plumule.

[2] Comptes rendus, 1848, t. xxvii. p. 226; Ann. des Sc. Nat., sér. 3 (1848), x. 207-237.

[3] Perhaps, instead of saying that *Schizopetalum* has four cotyledons, it would be more accurate to describe the two cotyledons as *lobed*. The cotyledon of the linden has five such lobes. Between these lobed cotyledons, and those which, as in Coniferæ, are divided almost to their base, there is an almost insensible gradation. In the rue, sycamore (*Acer pseudoplatanus*), &c., seedlings with lobed cotyledons are often seen.

[4] Masters's Teratology, p. 370-371, and the papers of De Candolle, Jaeger,

In *consistence*, the cotyledons may be fleshy; thick, as in the case of acorns, chestnuts, &c.; or thinner and more membranous. The fleshy cotyledons are found in exendospermous seeds, and the thinner or membranous in *endospermous* ones—the difference being due to the fact that, when the endosperm is not present, the cotyledons, from the nutriment stored up in them, furnish food for the young plant; while in the thin membranous cotyledons, in which their foliary nature is shown by the presence of nerves not easily seen (if at all) in the fleshy ones, the young plant is nourished by the stored-up endosperm.[1] As specimens of the fleshy cotyledons, the bean or acorn may be cited; while *Ricinus*, *Euonymus*, *Rubia tinctorum* (fig. 340), &c., afford good examples of the thin, delicate, flattened cotyledons, which, from their more perfect resemblance to leaves, have been called *foliaceous*. In such a case it is the endosperm which makes up the bulk of the seed.

(1.) In Dicotyledons, the cotyledons are in general opposed like ordinary leaves, and when two are present, are both of equal size. (2.) Sometimes, however, in some Malpighiaceæ, we find one increased in size at the expense of the other (as in *Sorocea*, *Hiræa*, and *Trapa natans*, where the large fleshy cotyledon constitutes the edible portion of the seed). When the embryo is coiled or folded, it is always the inner one which is smaller than the other. In some of the Cycadaceæ they are also somewhat unequal. (3.) In Dicotyledons, one may be even wanting altogether. In Lentibulariaceæ, *Abronia*, *Cyclamen* (in which genus the radicle is much enlarged), and *Corydalis solida* (Bischoff) generally this is the case; so that these are in reality monocotyledonous—so far as this character goes, though in reality dicotyledonous—as all other portions of their structure show them to be. (4.) Finally, in various parasitic flowering-plants—such as the dodder, *Monotropa*, *Rafflesia*, *Hydnora*, orchids, &c.—the list of exceptions finds its extreme,—these plants having no cotyledons at all.[2] In

---

Ehrenberg, Reinsch, and A. de Jussieu, cited there. Mr Meehan will even have it, "all seeds are primarily monocotyledonous, and that division is a subsequent act, depending on circumstances which do not exist at the first commencement of the seed-growth" (American Nat., 1871; and Nature, 1871, p. 153; Proc. Phil. Acad. Sc., April and May 1871).

[1] Van Tieghen, Note sur le divers modes de nervation de l'ovule et de la graine, Comptes rendus, lxxiii. (August 1871); Ann. des Sc. Nat., 5e sér., xvi. 228; Le Monnier, Ann. des Sc. Nat., 5e sér., xvi. 233.

[2] It is erroneous to describe, as is sometimes done, *Lathræa Clandestina* (Orobanchaceæ) as deprived of cotyledons. *Lecythis*, which Richard describes as wanting cotyledons, cannot also properly come within this category. The great division of *Acotyledons* is not, however, founded on such exceptions; but on ferns, lichens, mosses, fungi, sea-weeds, &c., which do not grow from seeds proper, and none of which have anything like cotyledons.

the dodder the embryo is of considerable size; but in most such parasites—*e.g.*, the mistletoe—the embryo is very minute, and reduced to a state of great simplicity, and seems to remain, until germination, in a very rudimentary state (Gray). (5.) In some dicotyledonous plants—*e.g.*, horse-chestnut (where they are well developed), *Tropæolum*, *Careya herbacea*,[1] Castanea, buck-eye (American species of *Æsculus*), various Cactaceæ—*Echinocactus*, *Echinopsis*, and *Phyllocactus*,—they are small and solidified in one mass; but in *Opuntia*, *Cereus*, &c., the cotyledons are separated and tolerably well developed—two Dicotyledons are more or less consolidated or coherent by their contiguous faces (conferruminate).[2]

In the case of the chestnut it is, however, generally more or less easy to trace the line of connection between the cotyledons; but in the other examples of conferruminate cotyledons which we have given, this is by no means so easy, if possible—the cotyledons being solidified into one mass instead of having their contiguous faces in contact, as in the first example. In form the cotyledons[3] are very varied,—being *rounded*, *elongated*, *linear*, *winged*, *obtuse;* and though in general sessile and *entire*, may be *lobed* (p. 511), *petiolate* (Geranium molle), *auriculate* (ash). We also find, as described in some of the foregoing examples, that most of the forms of the præfoliation of ordinary leaves are seen in the seed-leaves or cotyledons. They may be *conduplicate*[4] (cabbage, mustard, crambe, &c.), *reclinate* (p. 163), *convolute* (pomegranate), *circinate* (*Bunias* and *Erucaria*), *equitant* or *semi-equitant* (p. 163).

As to the *relation of the cotyledons* (in the dicotyledonous embryo) *to one another*—(1.) the two *faces* are usually applied to each other before germination, the *back* of the cotyledon being

---

[1] Griffith in Linnean Trans., xx. 270.

[2] Pseudo-monocotyledonous (Gärtner); macrocephalous (Richard).

[3] M. Germain de St Pierre is inclined to believe that in *Cyclamen* the single cotyledon, so called, is in reality developed by the gemmule, so that it would supply another instance of Dicotyledons being not monocotyledonous, as usually believed, but acotyledonous. He also asserts that *Bunium Bulbocastanum*, and other tuberous Umbelliferæ—notably *Biasolettia tuberosa*—germinate with one cotyledon. Probably, as the development of plants is more attended to, such exceptions will be found to be more common than is at present believed.

[4] Certain signs have been used to express the different methods in which the cotyledons are folded, these variations being used as characters to divide the order Cruciferæ into tribes. For instance, *conduplicate* is distinguished by O >—*i.e.*, bent longitudinally, so as to form a groove, in which the radicle is placed, characteristic of the Orthoplaceæ; *accumbent* by O =; *incumbent* by O ||; *circinate* by O || ||, characteristic of the tribe Spirolobeæ. In the division Diplicolobeæ, the cotyledons are folded twice upon themselves, as seen in *Senebiera*, *Subularia*, and *Heliophila*, such an arrangement being expressed by the sign O || || ||.

considered the convex portion turned outward. (2.) In some rare cases (as in some Ranunculaceæ, and the genera *Monimia* and *Boldea* among the Monimiaceæ), the two cotyledons are turned out from one another. (3.) In some seeds of the order Combretaceæ, in the pomegranate, the cotyledons are spirally rolled on their axis. (4.) Sometimes "the embryo, having a more or less elongated shape, rolls upon itself in forming a spiral, the turns of which are placed on the same plane" as in certain Cruciferæ, particularly in the genus *Bunias* (Richard).

The *epidermis* of the cotyledons differs in structure, according to the function which it is required to fulfil. (1.) If the cotyledons are *hypogeous*—*i. e.*, remain concealed in the ground (p. 527)—their surface absorbs the endosperm when this exists, and increases in size in a ratio proportionate to the rapidity of absorption (*e.g.*, in palms, grasses, &c.) In such cotyledons the epidermis is delicate; and numerous vascular bundles in the midst of a parenchyma, gorged with juices, favour this function of absorption. (2.) If, on the contrary, the cotyledons are *epigeous* (p. 527)—or rise above the ground to furnish the first "seed-leaves"—they are, like ordinary leaves, furnished with stomata to a greater or less extent (*e.g.*, beet) on both surfaces, or at least on one of their surfaces (*e.g.*, beech and birch). However, if the cotyledons increase by the absorption of endosperm, then the face

Fig. 342.—A male plant of *Stangeria paradoxa*, one of the Cycadaceæ. The flowers are diœcious; in the male plant they are reduced to very small ovoid anthers, opening by a longitudinal slit, borne in great numbers on the inferior face of the scales of large terminal cone-like catkins.

in contact with the endosperm is not provided with stomata (Coniferæ).

NAKED SEEDS.

Hitherto the seeds which we have been describing are enclosed within a pericarp; and hence the plants having their seeds so arranged within seed-vessels are called *Angiospermæ*.[1] In Coniferæ (figs. 124, 125, p. 187) and Cycadaceæ (figs. 342-345), however, the pistil is formed of a single carpellary leaf, which is entirely open and exposed, and thus leaves the ovules *naked*. Such ovules producing naked seeds, not contained in a pericarp, are characteristic of that section of flowering-plants which, on that account, are called *Gymnospermæ*.[2] In Ephedras (joint-firs)[3] and junipers, the seed is surrounded by a fleshy arillus, and accordingly looks like a berry. The juniper "berry" (fig. 346) contains three seeds, whilst that of the *Ephedra* and yew only contains one. In *Podocarpus* it is the extremity of the branch which swells out and becomes fleshy, as in the fruit of Anacardium; it is then the funiculus. The wings of the

Fig. 343.—Scale of *Ceratozania robusta*, one of the Cycadaceæ, bearing naked seeds at its base.

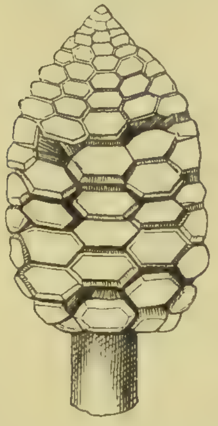


Fig. 344. — Cone of *Dioon edule*, one of the Cycadaceæ (1-7th nat. size.)

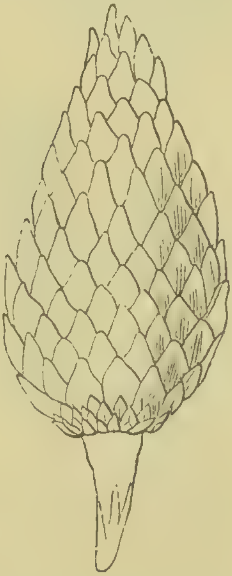


Fig. 345.—Cone of *Zamia integrifolia*, one of the Cycadaceæ (½ nat. size).

---

[1] ἀγγεῖον, a vessel; σπέρμα, seed.

[2] γυμνὸς, naked; and σπέρμα.

[3] Mr J. Miers considers that *Ephedra* is improperly placed among Gymnosperms, and maintains that it has neither naked ovules nor naked seeds, and is more allied to the *Urticaceæ* than to the *Cycadaceæ* or *Coniferæ* (Contrib. to Botany, vol. ii., 1869).

seeds of firs (Abietinæ) are prolongations of a part of the scale which accompanies the seed (fig. 125, p. 187). This opinion regarding the gymnospermy of the Coniferæ was first promulgated by Robert Brown in 1825,[1] and since then has been adopted by the greater number of botanists, among whom Lindley, Brongniart, Endlicher, Richard, Schleiden, Caspary, Schacht, Alphonse de Candolle, Sperk, Sachs, Duchartre, Hooker, and Bentham, are in the first rank. An opposite opinion has, however, been promulgated by Mirbel, and supported by Agardh, Spach, Payer, Parlatore, Baillon, Strasburger, and a few others of less note (or of no note at all). According to them, it is the seed-integument, not the carpellary envelope, which is wanting. From this point of view, the ovary of Coniferæ is made up of two carpels without floral envelopes, containing an orthotropal ovule placed upright on a basilar placenta.

Fig. 346.—Juniper (*Juniperus communis*) fruit-bearing fronds, with details of the flower and fruit.

The cup of yew, &c., which has been considered an arillus, is, in this opinion, a production anterior to fecundation, just as the floral organs called discs are the result of the expansion of a consecutive axis.[2] Such naked seeds must necessarily be impregnated in

---

[1] Targioni-Tozzetti, however, as early as 1810, enunciated very similar views as Caruel pointed out in 1865 (Strasburger, Coniferen, s. 174).

[2] In respect to this question the student may consult, as regards Coniferæ, the following papers and separate works (regarding origin of embryo and fecundation): R. Brown in Brit. Assoc. Rep., 1834, and Collected Works (Ray Soc.); Hartig, Forstl. culturpfl. (1840), t. xxv.; Geleznoff in Ann. des. Sc. Nat., sér. 3, xiv. (1850) 207; Hofmeister in Development of the Higher Cryptogamia (trans. by Currey in Ray. Soc. Publicns.); Schacht, Lehrbuch, Bd. ii. p. 401, and Der Baum, ed. 2 (1860), p. 273; Mohl in Verm. Schrift, s. 45 (on fruit-bearing scales); Caspary, De Abietin. fl. fem. (1861), and in Ann. des Sc. Nat., sér. 4, xiv. 200 (regarding the ovule, naked or within an

the state of ovules without the intervention of style or stigma, or any stigmatic apparatus (p. 414). With the exception of the orders named, we know of no other instances of true naked seeds. In *Ophiopogon spicatus*, *Leontice thalictroides*, *Peliosanthes Teta*, &c., Robert Brown has, however, pointed out something in reality very similar. In these plants the ovules rupture the ovary at an early period of growth, and thus are, when ripe, really naked seeds; and in *Reseda*[1] the seeds are almost uncovered after the ovary begins to swell. The seeds of some plants will occasionally protrude, owing to the bursting of the fruit (*e.g.*, grapes), and ripen in that situation. By Linnæus and the older descriptive botanists, the term "naked seeds" was applied to the small seed-like fruits of Labiatæ, grasses, sedges, &c.; but the term was manifestly incorrect, as such "naked seeds" are all covered with pericarps. Accordingly, the expression is now never applied except to express the true naked seeds of Conifers, &c., just described.

---

ovary); R. Brown "On the Structure of the Unimpregnated Ovule," in Appendix to King's Voyage (1825), or in Collected Works (Ray Soc.); D. Don in Trans. Linn. Soc., xviii. 163 (1838); Eichler in Flora Brasiliensis, fas. 34, p. 441; E. Favre in Ann. des Sc. Nat., sér. 5, iii. 379; Sperk, Die Lehre v. der Gymnospermie im Pflanzenreiche (1869); and various papers by Hartig, Hofmeister, Caspary, Schacht, already quoted, as well as others by Lindley Endlicher, Mohl, A. Braun, Eichler, and others in various works, in advocacy of the gymnospermy of the Coniferæ: while the following papers advocate the doctrine of a closed monospermous ovary, as existing in this and allied orders (Gnetaceæ, &c.),—Rich., Mem. Conif. et Cycad., 1826; Mirbel and Spach (l. c.); J. G. Agardh, Theor. Bot. (1858), p. 317-323; Heinzel, Nov. Act. Nat. Cur. (1844), xxi. 1, 203; Baillon, Rec. d'observation, i. (1860); Alex. Dickson in Edin. New Phil. Journ., July-Oct. 1861, p. 183, and Trans. Bot. Soc. 1861; Parlatore in Comptes rendus, 9th July 1860 and Feb. 1861, Studii organ. dell. Conif. (1864), and De Candolle's Prodromus Par., xvi. (1868); J. D. Hooker on *Welwitschia*, Trans. Linn. Soc., 1862; and W. M'Nab on the Development of Flowers of *Welwitschia* in Trans. Linn. Soc., xxviii. 507 (Dec. 1872); A. S. Œrsted in Naturh. Forenings Vidensk. Meddel. Kjöb., 1869; Hofmeister in Vergl. Unters., 1851, and Jahrb. f. wiss. bot., i. s. 167; Strasburger, Die Befruch. der Coniferen, 1869: (on the pollen) Schacht in Jahrb. f. wiss. bot., ii. s. 142; Strasburger in Janaische Zeitschr. Bd. vi.; Pfitzer, Niederrh. Ges. f. Nat. u. Heilk., 7th Aug. 1871; Reinke in Göttinger Nachrichten, 1871, p. 350; and Sachs in Lehrbuch, 436 *et seq.* The following references relate more especially to the Cycadaceæ:—(regarding the development in general) Karsten, "Organogr. Betracht der Zamia muricata," in Abhandl. Akad. Berl., 1856, p. 193-219; Regel. Bull Soc. Nat. Mosc., 1857, vol. i.: (in regard to germination) Miquel in Linnæa, Bd. xxi. p. 503: (regarding inflorescence and the nature of the scales in the strobilus) Mohl in Verm. Schrift, s. 45 *et seq.*; Gottsche in Bot. Zeit., 1845, p. 307; Kraus in Jahrb. f. wiss. bot., iv. s. 329; Geyler, ibid., vi. s. 68; Thomas, ibid., iv. 43: (regarding the ovule and embryo) Miquel in Ann. des Sc. Nat., sér. 3, iii. (1845) 195; Arthur Gris in Bull. Soc. Bot. Fr. (1866), xiii. 10; Dippel, Bot. Zeit., 1862 and 1863; Rossmann, Bau des Holzes (1863); Abstract of Eichler's views by Wright, Trans. Bot. Soc. Edin., xi. 535; &c.

[1] Such seeds are called *seminude*.

Let us now, in concluding this account of the structure of the seed, sum up the characters of the embryo in the two great divisions of plants.

Dicotyledonous Embryo.—Its essential character consists in the fact that, as a rule, it has two cotyledons, and a naked radicle which elongates to form the root. In form it is extremely variable—being often ovoid, or almost globular, even flat, or finally cylindrical or very slender, an elongated ovoid being the most common form (fig. 341). The radicle is under the form of a minute conical elevation, which does not represent anything but a small part of the embryo, which is almost entirely made up of the cotyledonary bodies. More rarely, as in the genus *Pekea*, it is the portion most developed, and in such a case the cotyledons are very small. The form of the cotyledons varies much, and their thickness is greater or less, in proportion as the endosperm is found in greater or less quantity; and above all, when it is altogether wanting, the gemmule is always placed on the summit of the caulicle, which is, however, often not very naked. This gemmule is covered by the cotyledons, placed face to face; more rarely the two cotyledons are united together so as to form a more or less undivided body, as in the case of the horse-chestnut.

Monocotyledonous Embryo.—Here the embryo is very simple, consisting of a single cotyledon, and most frequently does not show a marked distinction into radicle, cotyledon, and plumule; but, as in *Iris* and *Triglochin* (palustre), is only a "homogeneous, undivided, cylindrical, or club-shaped body." In grasses, especially in cereal grains, the plumule is more manifest and complex, showing as it does the rudiments of several concentric leaves, or a well-marked bud even, before germination.[1] In other plants, however, such as the iris, onion, &c., there is nothing like a distinction of parts until germination commences. The form of the embryo is very varied (ovoid, depressed, cylindrical, &c.), but in most cases it is ovoid or oblong, or more or less obtuse at its two extremities. The single cotyledon, and the radicle sheathed by a *coleorhiza* (p. 529, fig. 348 *c*), or lips of the passage through which they protrude from the radicular extremity, are the two chief

---

[1] In wheat and some other grasses the caulicle has at its base in front, a great lateral projection (fig. 351 *g*, the *Scutellum* of Gärtner); but this is apparently another of the exceptions we have spoken of—viz., a second rudimentary cotyledon, and not the primordial radicle, as L. C. Richard thought,—or, according to Adrian de Jussieu, a special modification of the caulicle, to which the former botanist applied the name of *hypoblastus*. Lindley broached a theory, which in its main features has been adopted by A. de Jussieu (Ann. des. Sc. Nat., 2d ser., xx. 350), that the embryo of a Monocotyledon—a palm is the specimen he takes—is "analogous to that of a Dicotyledon of which one of the cotyledons is abstracted, and the other rolled round the plumule and consolidated at its edges."

characters distinguishing it. The embryo is contained in a little vaginal cavity at the base of the cotyledon, usually opening by a small longitudinal slit. The form of the cotyledon varies much. It is, however, generally cylindrical, even in embryos accompanied by an endosperm.[1]

In *Cryptocoryne spiralis*[2] there is an exception to the monocotyledonous character of the division to which it belongs; but all such exceptions are only peculiar modifications of structure, and do not invalidate the general rule, or warrant us in altering the names applied to the great division of plants founded on the prevailing character.[3] As regards development in Orchids, Monotropaceæ, Pyrolaceæ, Orobanchaceæ, Rafflesiaceæ, Balanophoraceæ, and *Hydnora*, the embryo is very simple, consisting of a spherical body made up of a few cells. In Monocotyledons in general it is more complicated, it being possible to distinguish the plumule and the cotyledon which surrounds it, and at the radicular extremity a tissue in which the radicles are developed (figs. 347-352). In Dicotyledons the embryo attains the highest development before germination—the two cotyledons, plumule and radicle, being in nearly all cases well marked (fig. 339), though there may be cases where there is, as in *Cyclamen* and *Trapa*, only one developed cotyledon, or even none (p. 512).[4]

---

[1] Achille Richard, lib. cit., p. 295.

[2] Griffith, Linn. Trans., xx. 271.

[3] For instance, Cassini proposed to style Dicotyledons *Isodynamous* or *Isobrious*, and Monocotyledons *Anisodynamous* or *Anisobrious*, because in the first the force of development is equal on both sides, and because in the other the force of development is greater on one sort than the other, resulting in the single cotyledon. The student has already seen that there are plenty of exceptions to this rule, so that in point of accuracy of nomenclature the one series of names is as faulty as the other. Again, Lestiboudois calls Dicotyledons *Exoptiles*, and Monocotyledons *Endoptiles*, because in the first the plumule is naked, while in the latter it is enclosed within the cotyledon. Perhaps more correct were the terms *Endo-* and *Exo-rhizal*, proposed by Richard for the two divisions; for in reality the fact of the radicles being sheathed as they pass out of the radicular extremity of the seeds, is the only invariable distinction which separates Monocotyledons from Dicotyledons. Dumortier's terms of *Endo-* and *Exo-phyllous* were of parallel value, being founded on the distinction afforded by the fact that in the first division (Monocotyledons) the leaves are evolved within a sheath (*Coleophyllum* or *Coleoptilum*), while those of the second (Dicotyledons) are always naked. Of making names there is no end—a fact which might be to the advantage of botanical science if the end of the accumulation of facts was simply that names might be applied to them; but as the object of names is only to facilitate the remembrance and recording of facts in something like a system, the value of one name over another is not of particular moment, except in so far as it may be more convenient than the other. This does not apply to the names quoted.

[4] In Monocotyledons, Hofmeister has laid down the law, that in vertical seeds, whether erect or pendulous, the medial plane of the cotyledons coincides with that of the seed, while in horizontal seeds the plane of the cotyledon is at

The further distinctions as regards developments we will reserve until we have occasion to speak of the process of germination (p. 527). In the mean time, let us speak of the conditions of the seed necessary to that process being performed ; and first, regarding the

GROWTH OF THE SEED.

A seed attains its maximum size at an early stage of its growth. After this the tissues within the spermoderm solidify as the seed ripens, without, however, any further increase in size. There is even a decrease in the dimension of the seed as it ripens, by the contraction of the exterior, in this respect somewhat resembling the pericarp of some fruits. That the outside dimensions of the seed should be the parts which first arrive at maturity, it is necessary that the parts in the interior should have room to increase and solidify. After the secondary parts have thus attained their maximum size, the embryo and the endosperm, which are the primary parts of the seed, become the chief centres of growth. The shape of the seed is greatly determined by the relative rapidity of the growth of parts.

Ripening of Seeds.—Seeds are in their early state green—and even the embryo is so also ;[1] but when they ripen, the exterior gets paler, whitish, white, or yellowish brown, owing to changes in the contents of the cells of the spermoderm. Some seeds are diversified, and often brilliantly variegatedly coloured, as we have a familiar example in the different varieties of kidney-beans. The bright glistening appearance of immature seeds is owing to the presence of water in the spermoderm, and it decreases as the amount of water diminishes by drying, though some seeds are bright even when mature, owing to a peculiar condition of the epidermal cells, or perhaps to the presence of some oily or waxy substance.

The decrease of the dimensions of the seed as it ripens is owing to the loss of water, on account of less and less sap arriving in the seed as it gets ripe, the result of which is the atrophy of the funiculus. The amount of water in dry seeds is about 4 per cent on

---

right angles to it ; but in the date-palm, where the slit of the cotyledon is a vertical one situated near the base of the cotyledon, Professor A. Dickson has pointed out that there is presented an exception to the invariability of that rule (Nature, 1870, p. 38). The most recent research on the development of the embryo in Monocotyledons and Dicotyledons is one published as these sheets are passing through the press—viz., by Johannes Hanstein (Botanische Abhand., Heft i.), which I have only seen in an abstract (by Dr M'Nab) in Month. Journ. of Mic. Sc., 1873, p. 51.

[1] Some embryos, even in the ripe seed—*e.g.*, mistletoe, *Pistachia*, some Cruciferæ, &c.—remain quite green.

an average, but it varies in amount from 8.50 per cent in seeds of wild plants of *Barbarea præcox*, down to 0.50 in those of *Erysimum officinale.*

Ripe seed is usually denser than the unripe seed, to the extent that it will sink in water; hence the common test for it. The less density of unripe seed is owing to the imperfect or entire want of development of the embryo; hence it floats. This test is not, however, infallible; for some perfectly ripe and sound seeds will float also. The density of seeds varies, according to the observations of Schübler and Renz, from 0.210 up to 1.450; while those of others, like some Leguminosæ, Polygonaceæ, Amarantaceæ, grasses, &c., sink before being ripe (Duchartre). It is always of importance for the cultivator to know what value is to be attached to seeds. If, for example, he finds that only two-thirds of his seed will germinate, then he must sow a corresponding quantity over a given extent of ground. To test the germinating power, the following procedure, recommended by the eminent French agriculturist Matthieu de Dombasle,[1] may be useful :—

"Cover the bottom of a saucer or plate with two pieces of rather thick cloth which have been wetted, and place the one over the other. Spread on this a certain number of seed, taken at random from the package to be tested, each seed being separated by a small space from its neighbour. Then cover them with a third piece of cloth like the first two, and wet it. Now place the plate in some moderately warm place, such as on a chimney-piece, or in the vicinity of a stove. As the cloths begin to dry, wet them again, but allow no surplus water to accumulate about the seeds; and accordingly, after the cloths have absorbed all they can, pour off the surplus by raising gently the plate from the horizontal. The progress of germination can be watched day by day, by simply raising up the topmost piece of cloth. Those seeds which have lost the power of germinating will generally in a short time get covered with moulds."

---

[1] Moniteur du Soir, 7th March 1867 (quoted in Cave's Cours Elémentaire de Botanique, p. 102).

CHAPTER XII.

GERMINATION.

BEFORE investigating the nature of the process of germination, or "sprouting," it may be well to discuss a few points regarding the vitality of seeds—a subject which is of the greatest importance, not only in physiological but in geographical botany.

Duration of Vitality.—If seeds are kept dry, the embryo remains dormant; but the time during which the embryo will retain its vitality varies much with the seeds of different species. For instance, it is said that the seeds of willow will not grow after having been once dry, and that if even kept fresh they lose their germinating power in two weeks. The seeds of coffee and other *Rubiaceæ*, *Angelica*, and other Umbelliferæ, do not germinate freely after having been kept for any length of time. The seeds of wheat usually lose the power of growth after being kept seven years, though it has been found quite capable of being used as food even after being kept more than two centuries. The stories about "mummy wheat" sprouting after remaining in Egyptian tombs for thousands of years are, to say the least of them, very dubious, no well-authenticated instance of such being extant; while among other articles sold by the Arabs to credulous travellers, as coming out of the same tombs as this ancient wheat, have been *dahlia bulbs* and *maize*—the deposition of which in the receptacles from which they were said to be extracted necessitating the belief that 3000 years ago the subjects of the Pharaohs were engaged in commerce with *America!* Dietrich[1] experimented with the seeds of wheat, rye, and a species of *Bromus* 185 years old, but failed to induce them to germinate, the place of the embryo being occupied by a slimy putrefying fluid.

If, however, excluded from the air, damp, &c., seeds have been known to keep for somewhat lengthened periods. For instance, those of leguminous plants have been known to sprout after being kept dry for 60 years. In 1810, fruit was obtained in the Jardin des Plantes from a species of *Phaseolus* or *Dolichos* taken from

---

[1] Hoffman's Jahresbericht, &c., 1862-63, s. 77 (*fide* Johnson).

the herbarium of Tournefort, who flourished about 1694. The seeds of the sensitive plant have germinated after being kept 60 years; while Gerardin records that haricot-beans, after being kept for more than 100 years in herbaria, sprouted. Rye has been said to have sprouted after 140 years (Home). Alphonse de Candolle found, from experiments in the Geneva Botanic Garden, that large seeds keep longer than small ones, and that the germinating power of seeds was in an inverse ratio to the rapidity of germination.[1] The seeds of woody species seemed to preserve their vitality longest, and biennials shortest; while those of perennials were longer-lived than those of annuals. Seeds of the ordinary *Rubus Idæus*, or raspberry, found in a British tumulus near Malden Castle, Devonshire, in 1834, along with coins of the Emperor Hadrian (and therefore, *if contemporaneous*, sixteen or seventeen hundred years ago), germinated under the care of Professor Lindley, and produced vigorous fruiting plants. M. Charles Desmoulin also generated seeds of *Medicago lupulina*, *Centaurea Cyanus*, *Heliotropium Europæum*, &c., found in Roman tombs dating most probably to the second or third century of our era. Numerous instances are recorded of seeds which have been supposed to be buried in the soil under old houses springing up; but most of these cases must be viewed with a certain degree of scepticism, the openings for error or deception being too many. As one specimen, I quote the following instance, communicated in 1866 to the Botanical Society of France, and said to be authentic: Under the foundations of a very ancient building demolished recently in the "Ile de la Seine" where the city was founded, Dr Boisduval took a quantity of blackish earth, in the midst of which an attentive examination revealed the presence of seeds. These seeds, grown with great care under a bell-glass, or "cloche," gave origin to plants of *Juncus bufonius*, L., a plant of moist places and grounds inundated during the winter—*i. e.*, growing ordinarily in conditions similar to that presented by the ground on which was built the ancient city of Lutetia! Gilbert White long ago noted that, when beech-trees were cleared off from the "Hanger" at Selborne, the ground got covered with strawberry plants, which might have probably lain in the ground for many years, but could not vegetate till the sun and air were admitted; and that places, where in his day, and for a century before, beech-trees had grown, were known to the people by the name of strawberry "slides" or trenches, though no strawberries had grown there in the memory

---

[1] Sur la durée de la faculté de Germiner, &c.; Ann. des Sc. Nat., 1846 (t. vi.), p. 373-382; Ann. Nat. Hist., 1st ser., xx. 38; Lefebure, Sur la Germination des Plantes, 1804; Gerardin, Sur la propriété des Graines de conserver longtemps leur vertu germinative, 1809; British Assoc. Rep., 1850, p. 62; &c.

of man.[1] In some experiments made in 1817 by Sir Thomas Dick Lauder, he found that four species of plants (*Hieracium pilosella*, *Myosotis scorpioides*, *Lamium purpureum*, and *Spergula arvensis*) germinated in soil taken from beneath a covering of sand, which had lain over a portion of Morayshire for at least sixty years.[2] Numerous such cases could be quoted. For instance, maize from the tombs of the Incas of Peru—and therefore probably at least 300 years old—has been known to germinate. Seeds of ragwort taken from the centre of a solid mass of peat-earth, at a depth of 16 feet, in a bog in the Isle of Man, have germinated. Some hazelnuts, discovered at a considerable depth in a morass in the county of Durham, grew when sown, &c.[3]

Kemp[4] records an instance of having germinated seeds of *Polygonum Convolvulus*, *Rumex Acetosella*, and an *Atriplex*, taken from the depth of 25 feet in a sand-pit near Melrose, and in regard to which he had satisfied himself that there had been no deception or error. He considered that they might have been more than 2000 years old. Mr Grugeon has communicated to me a similar instance of vitality in buried seeds of a *Rumex*. It therefore appears that if seeds are buried at a depth in the soil where they may be removed from the influence of light, heat, oxygen, and other conditions of germination, they may preserve their vitality for a considerable period; but there are so many probabilities of mistake or collusion to be eliminated, that any extraordinary cases of vitality reported require to be carefully examined before anything like implicit credence is given to them. On the whole, it may be said that the rule is, that the fresher seeds are, the more certainty there is of their germinating, and that the percentage which spring is in a tolerably direct ratio to their age.[5]

Londet and Haberlandt made experiments with cereals which proved this decisively. The following table gives the results of the latter observer :—

---

[1] Nat. Hist. of Selborne (Blyth's ed.), p. 300.

[2] Macgillivray, Edin. Journ. of Nat. Hist. and Phys. Sc., 1836, p. 35.

[3] These and various similar facts are given at length in an anonymous little work published at Edinburgh in 1835, entitled the 'Physiology of Plants; or, the Phenomena and Laws of Vegetation,' which contains some original matter worthy of attention.

[4] Ann. of Nat. Hist., 1st ser., xiii. 89.

[5] The vitality of seeds will be discussed at greater length in PHYTO-GEOGRAPHY.

Name of grain.	Percentage of seeds that germinated in 1861, from the years						
	1851.	1854.	1855.	1857.	1858.	1859.	1860.
Wheat, . . .	0	8	4	73	60	84	96
Rye, ...	0	0	0	0	0	48	100
Barley, ...	0	24	0	48	33	92	89
Oats, ...	0	56	48	72	32	80	96
Maize, ...	—	76	56	—	77	100	97

Results of the Use of long-kept Seeds.—Old seeds yield weak plants, and this peculiarity is taken advantage of by horticulturists in producing new varieties. It is said that while one-year-old seeds of the ten-week stock yielded single flowers, those which had been kept four years produced, for the most part, double flowers, which are a monstrosity, the result of feebleness in the constitution of the plant (p. 385). From observations made at the instance of the Prussian Horticultural Society by Schmidt, Sprengel, D'Arenstorff, Treviranus, and Voss, it has been found, as a general result, that in the case of melons and cucumbers, the longest-kept seeds, though less certain to germinate, yet yielded the greatest amount of fruit ; while new seed produced vigorous plants, which ran too much to leaf.[1] M. Voss reared, from 24 seeds of a Spanish melon thirty years old, eight plants which gave good fruit. Cucumber-seeds 17 years old gave the same result ; while some seeds of *Althæa rosea* (hollyhock) 23 years old afforded well-conditioned plants. It was found, by most of the above observers, that plants obtained from the seeds of the preceding year produced many leaves but few fruitful flowers, and almost entirely male ones ; but that these same seeds, dried by the heat of the sun or of a stove, yielded a greater number of fruitful plants, and that it is particularly at the end of some years they acquire this property. Erasmus Darwin accounts for the greater fruiting powers of old seeds by supposing that the cotyledons may receive some damage from keeping, which prevents their nourishing the young plant at its first germination so perfectly as they could otherwise have done.

Treviranus argued stoutly that unripe seeds could not germinate

---

[1] I am informed by my friend Mr Wm. Gorrie, of Trinity, Edinburgh, a very experienced scientific agriculturist, that the same fact has been noticed among agricultural plants. For instance, the late Mr Oliver, of Lochend, near Edinburgh, found that two-year-old turnip-seed produced larger bulbs and less leaf than fresher seed. The ordinary garden balsam also produces more flowers and less leaves if kept some time than if sown the first year.

—and certainly the common-sense prejudices of ordinary observers were with him. But this has been shown to be erroneous. Duhamel germinated green seeds of the oak; Senebier, green peas; Seiffert, haricot-beans, lentils, peas, broom, &c., which were not half grown; and the *Styphnolobium* of Japan, which cannot ripen its seeds in the Breslau Gardens, is nevertheless, according to Göppert, multiplied by incompletely-developed seeds. The only difference is, that these unripe seeds are a little longer in germinating than the ripe ones. Various observations have been made by Göppert, Duchartre,[1] and others, with cereals and cultivated grasses, with a similar result. Again, we are told by Von Martius that the Brazilians always propagate *Willughbeia speciosa* by unripe seeds, considering that the fruit from plants thus obtained is better than that from trees grown from matured seed. It appears, therefore, that the faculty of germination does not depend upon the seed having attained its maturity, but dates to a period anterior to this. In plants belonging to many natural orders, the seed can germinate when it has advanced but a short way to maturity; but it is necessary that the embryo should have advanced some considerable way, and that the albumen has taken some degree of consistency. In general, Ferdinand Cohn found that plants reared from such seeds were not feebler than others.[2]

Unripe Seeds.—All authors are, however, agreed, that if seeds are gathered when unripe—even when the kernel is soft and milky, or even before the starch has formed and the kernel is like water in appearance—they are "capable of germination if allowed, after ripening, to dry in connection with the stem." Many, however, do not come up: and at first those which do germinate yield weak plants, and give a poor harvest in poor soil; but in rich soil the crop is as vigorous as that produed from ripe seed.[3] The sowing of unripe peas produces earlier varieties. In the words of Liebig, " the gardener is aware that the flat and shining seeds in the pods of the stock gilly-flower will give late plants with single flowers, while the shrivelled seeds will furnish low plants with double flowers throughout."

Dwarfed or Light Seeds.—Light seeds sprout quicker, but yield weaker plants, and are, in addition, not so sure of germinating as heavy grains. The number of roots, and the strength of these roots formed in the process of germination, are (as regards their non-nitrogenous constituents) *in direct proportion to the amount of starch in the seed.*[4] We must, however, remember

---

[1] Expériences sur la germination des Céréales, Journal d'Agric. pratique, 1853, 3e sér. (t. vi.), p. 177-180.

[2] Beiträge zur Phys. der Samens; Flora, 1849; and Symbola at Seminis physiologiam, 1847 (Berlin), which I only know from quotation.

[3] Lucanus, Versuch.-Stat., iv. s. 253.

[4] Liebig, Nat. Laws of Husbandry, Engl. trans. (1813), p. 7.

that the vigour of plants is not altogether dependent on the causes we have sketched out in the preceding pages, but that allowance must be made for the depth of soil they are laid in, and the stores of nourishment the plant may find there when it first begins to lead an existence independent of the seed.

Value of Seed as regards Density.—Church found, from his experiments at Cirencester, that the value of seed-wheat stands in a certain connection with its specific gravity, and that (1.) the seed-wheat of the greatest density produces the densest seed; (2.) that the densest seed produces the greatest amount of dressed corn; (3.) seed-wheat of medium density generally gives the largest number of ears, but the ears are poorer than those of the densest seed; while, again, (4.) seed-wheat of medium density generally produces the largest number of fruiting plants. Though I am not aware that these and other observations made by this eminent chemist have yet been repeated by any other observer, the care with which they were made precludes the likelihood of any error.[1]

THE ACT OF GERMINATION.

In order that the young plant or embryo may burst the coverings around, and take the first steps to becoming the future plant —in a word, that it may germinate—certain conditions are necessary. In the first place, it must be deposited in the soil, or other element in which it is intended that the plant should grow and extract nourishment from. By sowing the seeds in a box of earth or sawdust, or even on a damp sponge, we can trace all the processes of germination. The seeds absorb water and swell, the embryo enlarges beneath the seed-coat, and shortly the integuments burst and the radicle appears, when afterwards the plumule makes itself manifest. The endosperm always, and the cotyledons —if the seed has no endosperm, as in many plants (horse-bean, pea, maize, barley)—remain in the place where the seed was first deposited, and the first leaves grow out of those of the plumule (hence called hypogeous).[2] In this case the store of nutriment is in the cotyledons. In others—such as kidney-bean, buckwheat, radish, &c.—the cotyledons ascend and become the first pair of leaves (epigeous).[3] These leaves are generally differently shaped from the others, and undivided, though in the vine there is an

---

[1] For full account, see the Cirencester Agricultural Essays, edited by the Rev. J. Constable, entitled Practice with Science, 1867, p. 107, 342, 345; and abstract in Johnson, op. cit., p. 295.

[2] *ὑπό*, under; and *γῆ*, the earth.

[3] *ἐπί*, upon; and *γῆ*.

exception. In the former case the rudimentary stem or radicle scarcely elongates at all; in the latter it grows throughout its entire length, and elevates the cotyledons above the soil, the ascending plumule shortly unfolds new leaves, and if coming from the seed of a branched plant, lateral buds appear. The roots are formed at the end of the radicle. After this the young plant ceases to draw nourishment from the seed. Then the process of germination is finished, and the plant leads an independent existence. A second internode, bearing a second pair of leaves, is formed. This, like its predecessors, lengthens, and carries up this second pair to some distance above the first. Then a third internode springs from between them, also crowned with its leaves,—and so on, until the herb is built up. From what we have already said in describing the embryo, it is unnecessary to go into further details regarding the process of germination. The process of germination is in Monocotyledons and Dicotyledons much the same, with the exception that in the former only one cotyledon is developed. The general characters of monocotyledonous germination can be well seen in the illustration of the germination of wheat (figs. 347-352). In some Monocotyledons—*e.g.*, the ivory palm—while certain soluble matters of the endosperm are consumed, the endosperm still retains its appearance in outline.

The name *proliferous* or *viviparous* plants is given to those from which buds can be detached, which will produce separate individuals, as seen in many grasses—*e.g.*, *Festuca ovina*, var. *vivipera;* and in the case of the axils or edge of various leaves—*e.g.*, those of *Bryophyllum*, &c.[1]

Conditions necessary to Germination.—We have seen that the vitality of the seed may remain dormant for considerable periods. During these more or less lengthened periods, the conditions essential to germination must have been wanting. Let us consider what are the conditions necessary to the seed germinating after it has once been deposited in the medium from which the young plant is intended to extract its nourishment. These we may discuss under the heads of (1.) temperature; (2.) moisture; (3.) oxygen; and (4.) light and darkness.

---

[1] In the bark of the beech, &c., are commonly found certain nodules, completely free and isolated, having a peculiar bark of their own, which is united with that of the parent tree, but which may in the cedar be easily distinguished by the direction of the fibres. Their form is varied; but the wood of these nodules is arranged in concentric zones round a common centre, and has both pith and medullary rays. Dutrochet, whose description we have quoted, looks on these as adventitious buds arrested in their formation; and the proof of their being of this nature is shown by the fact of their being employed in the case of the olive-tree, under the name of *Uovoli*, for propagation. Dutrochet calls them *embryo buds* (Mémoires, i. 310).

1. *Temperature.*—A certain degree of temperature is absolutely necessary before a seed will germinate; but this temperature must be confined within certain limits—above or below—or the vitality of the seed will be destroyed or dormant. Few seeds will germinate at a temperature of less than 4° Cent., at which Göppert succeeded in causing some to sprout. This is, however, lower than most seeds will germinate at. De Candolle,[1] for instance,

Fig. 347. Fig. 348. Fig. 349.

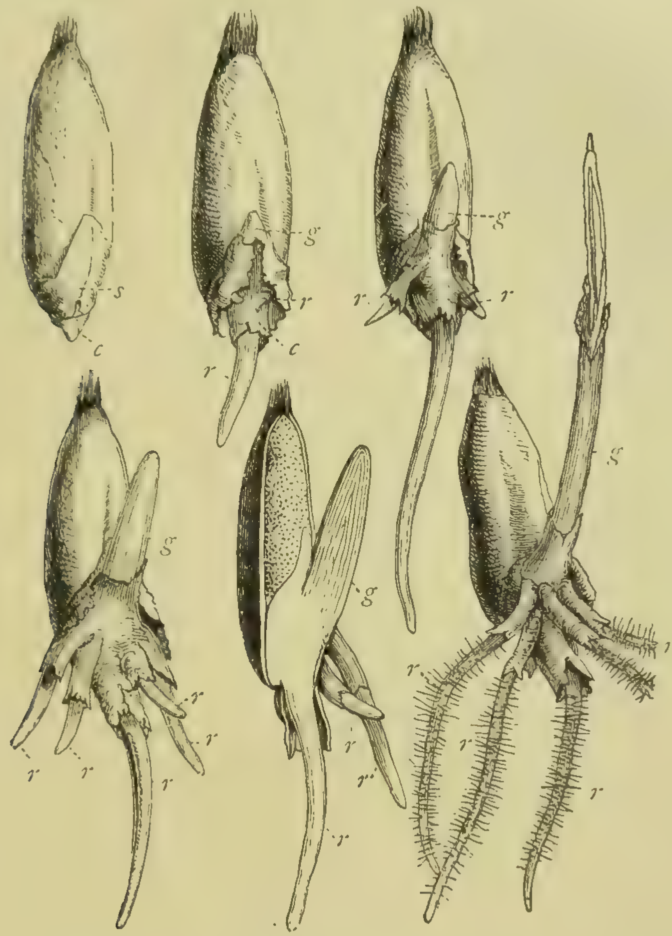


Fig. 350. Fig. 351. Fig. 352.

Figs. 347-352.—Illustrations of Monocotyledonous Germination. Fig. 347.—Caryopsis or grain of wheat, with the integuments resoftened; *s* Swelling of integument caused by the excentric embryo (p. 506); *c* Appearance of the coleorhiza or root-sheath. Fig. 348.—*r* The radicle, with the coleorhiza, *c*, around its base, when it passes out of the seed; the other radicles, *r r*, are as yet contained with the coleorhiza, and the gemmule, *g*, begins to make its appearance. Figs. 349, 350.—Here we see the parts, which are designated by the same letters as in the preceding figures, gradually increasing. Fig. 351.—Longitudinal section of fig. 350, to show the structure of the gemmule, *g*, and the presence of the endosperm. Fig. 352.—The plumule is elongated, surrounded at the base by its sheath, and the single cotyledon, *g*, raised above the soil (after Bocquillon).

---

[1] Bibliotheque Universelle, Nov. 1865.

could germinate none at a lower temperature than the freezing-point of water; and none of the agricultural seeds with which Sachs experimented would germinate below 5° to 13° Cent., up to 39° to 47°—above this degree the vitality of the seed was destroyed. Every plant has an intermediate point at which it germinates with the greatest success. Below that point the plant produced from the embryo is stunted; above, it shows an excited constitution, and is sickly and easily killed. The most favourable intermediate point for quickest germination of most plants is from about 78° to 93° Fahr.—any elevation above or below these extremes in general retarding germination. Edwards and Collin, who made many experiments on this important point,[1] found that the minimum temperature required for the germination of winter wheat, barley, and rye, was + 7° Cent. (44°6 Fahr.) In one of De Candolle's experiments, already quoted, he managed to germinate, at the freezing-point of water, two seeds of *Sinapis alba* (common mustard), in respectively 11 and 17 days. In another experiment he was able to germinate, between 1°4 and 1°9 Cent., *Lepidium sativum* and common flax-seed. Each species has, however, its own temperature. For instance, a graduated table of temperature at which seed will germinate could be formed from *Sinapis alba*, which germinated at freezing, up to the melon, which requires 17° Cent. (62°6 Fahr.) before its seeds will germinate. Again, up to a certain stage plants will germinate more quickly at a higher than at a lower temperature. For instance, mustard-seed, which took 17 days to germinate under a temperature of 32° Fahr., only took 1¾ days at 12°-13° Cent. (53°6-55°4 Fahr.); but at 17° Cent. (62°6 Fahr.) the seeds took 3½ days; while at 28° Cent. (82°4 Fahr.) only a few germinated; and at 40°-41° Cent. (104°-105°8 Fahr.) none whatever germinated.

Dry grass-seeds were found to germinate more freely than fresh ones after having been subjected to extremes of temperature. However, as starch-grains burst at 167° Fahr., it is found that seeds subjected to near that heat will not germinate—their vitality having been destroyed by the rupture of the starch-grains or their endosperm. Wheat, kidney-beans, and flax-seeds were killed in twenty-seven and a half minutes by water at a temperature of 143°6 Fahr.; rye and beans stood at a little higher temperature. Many seeds, but not those of barley, kidney-beans, and flax, bore a temperature of 125°6 Fahr. It was found that, in steam, seeds could bear a greater temperature than in water; and in dry air something more still. In sand or earth, wheat, rye, and barley bore 9° Fahr. more heat than in water, and indeed without inconvenience,—viz., seeds immersed in water at 35° Cent. (95° Fahr.)

---

[1] Ann. des Sc. Nat., 2d sér., Bot. i. (1834) p. 257-270.

for three days nearly all perished; while those in sand or earth sustained for a prolonged period 40° Cent. (104° Fahr.) It is probable, as Lindley[1] has pointed out, that these experiments throw light on the cause of the impossibility of making certain plants multiply themselves by seeds in hot countries. If wheat, barley, rye, &c., cannot endure a prolonged temperature above 104° Fahr.—and the temperature of the soil is in some countries and soils as high as 140° Fahr., according to Humboldt's observations—or between 118°4 and 122° Fahr.—as Arago asserts is the case in some parts of France—then it is evident that corn placed in such situations will perish. The cocoa-nut is said to germinate perfectly well in soil heated to 81° Fahr. In tropical plants naturalised in northern climates, a higher temperature can be borne by the seeds than can be endured by those native to these climates. It is probable that some arctic plants will germinate their seeds habitually at, or a very little above, the freezing-point.[2] The common chickweed in Britain must also often germinate its seeds when the temperature of the soil is hardly above freezing. Seeds have, finally, been known to germinate after being boiled. Australian acacias have been so experimented on; seeds of elder (*Sambucus*) have readily germinated after having been twice boiled in making wine—"had been present during the vinous fermentation, and had been allowed to remain among the dregs of the wine bunged up in the cask for a period of twenty months;"[3] and the seeds of raspberries have germinated after having been boiled in the process of making "jam."

Temperature has also, according to the observations of Sachs, an effect on the relative development of the parts of the seed, and thus influences the form of the plant. Low temperatures, for example, retard the production of new rootlets, buds, and leaves—while, however, the rootlets formed directly from the embryo become very long. On the other hand, very high temperatures cause the rapid formation of new rootlets and leaves, even before those existing in the embryo are fully developed. The medium temperatures most favourable for the germination of the seed are those which bring the parts of the embryo first into development; and at the same time, the rudiments of new organs are formed which are afterwards to unfold. Some seeds can be subjected to a temperature of 18° below zero (Fahr.) without the vitality being destroyed: wheat has been even subject to a temperature at

---

[1] Introd. to Bot., ii. 264.

[2] Many arctic plants do not, however, perfect their seeds, the plant propagating itself by roots. When arctic plants are taken to a warm country, unless they are kept for the first summer or two in a cold place, they rush to leaf, and often die off in the autumn.

[3] Hemingway in Annals of Nat. Hist., viii. 317.

which mercury froze without its vitality being destroyed; and grain has been dried under a temperature of 100° Cent. (212° Fahr.) without losing the power of germinating.[1]

2. *Moisture* is absolutely necessary for germination. Water is one of the main physical bases of life, and is the vehicle in which nutrition is conveyed to the young plant in the seed as well as in the soil. It assists in dissolving the dextrine, and other soluble substances in the seed, formed by the transformation of the starch of the endosperm for the nutrition of the embryo. It also swells out the albumen, and so assists in bursting the spermoderm, and thus supplies a passage to the radicle, &c. If the seed is contained in a hard pericarp, water also assists in softening and finally bursting this. For if the seeds are contained in a nut, water reaches the embryo with more difficulty; hence the slowness with which such "stone-fruits" germinate. Hence fruit-growers—as in the case of olives—sometimes find it to their advantage to break the stones before planting them. How does the water pass through the spermoderm? This has been the subject of no little controversy and experiment by Poncelot, De Candolle, Tittman,[2] and other phyto-physiologists; but it seems proved, by the observation of the last-named botanist, that it permeates through the whole surface of the spermoderm, if this is moderately soft, and if this covering is hard, through the micropyle and the hilum; the embryo only absorbs water by its radicle. De Saussure found that germination, once commenced, could be checked by desiccation, and then resumed if moisture was applied, as in most cereals, legumes, &c.; but seeds treated in this manner lose the radicle, and are less vigorous after being a second time fanned, by the aid of moisture, into life. We see a practical application of the utility of this property of seeds in the fact that, unless they possessed this power, crops sown in wet weather, and after germinating being subjected to long droughts, would inevitably perish. Some seeds, however, perish if the germination is once checked.

All seeds do not absorb the same amount of water; but most seeds absorb, in germinating, rather more than their own weight. Seeds of aquatic plants germinate naturally in water; others rot if the soil in which they are placed is too moist; while others are excessively intolerant of the presence of anything but the smallest amount of moisture in the soil.

3. *Oxygen.* — Free oxygen is also necessary to germination. Germination cannot proceed in a vacuum, or in an atmosphere of any other gas. If vessels are filled with nitrogen, hydrogen, carbon dioxide (CO_2), or any other gas, especially the last named, the embryo either lies dormant, or does not proceed with its

---

[1] Doyere, Ann. de l'Institut Agron., 1852, p. 269-379.

[2] Die Keimung der Pflanzen (1821), s. 47.

germination except in a hardly appreciable degree. Again, if water is deprived of its air, and therefore of the greater portion of its free oxygen, by boiling or distillation, seeds will not germinate in it unless, with the exception of some leguminous and aquatic species, it is continually agitated and renewed, to afford a fresh supply of oxygen. The part which oxygen plays in germination has been investigated by many observers,—first by Scheil in 1777; then by Rollo, Senebier, Huber, Ellis; but by none more ably than Theodore de Saussure,[1] whose researches have thrown much light on the subject. He showed that the oxygen absorbed during germination combines with the excess of carbon which is contained in the young plant, and forms CO_2, which is thrown off. It is by this absorption of oxygen that the starch of the endosperm, or of the fleshy cotyledons when the endosperm is not present, changes into dextrine, and then into sugar; and from being in an insoluble condition before germination, passes, in a soluble condition, to furnish the first nutriment of the embryo.

In pure oxygen there is little acceleration of germination. The quantity absolutely necessary for germination varies for different species—from about 0.01 of their weight, as in the case of haricots, beans, lettuce, &c., to barley, rye, &c., which require ten times as much. Too much oxygen, by combining with too much carbon, weakens the plant. The best admixture (1 of oxygen to 3 or 4 of nitrogen), as found by experiment, is just about the proportion of ordinary atmospheric air.

Seeds also take in a little nitrogen in germination. From the facts mentioned in the preceding paragraphs, the student will have seen that it is to get clear of the superabundant moisture about the roots of plants, and the accompanying coldness, that the farmer "subsoil" drains his land; and why seeds buried deeply in the soil, or otherwise placed beyond the reach of air by the surface of the soil being too firmly pressed, do not germinate; and they may also explain why seeds kept from the air retain their vitality for lengthened periods. On the same principles are also explained the alternation of forests if the soil is disturbed. Birches and aspens replace oaks and beeches. In North America poplars succeed firs; and herbaceous plants, hitherto unknown in the forest, spring up when it is cleared. The same fact has been noticed when the virgin forests of Brazil are burned over. In the isles of the New World deforested and cultivated for the first time, plants appeared formerly unknown in those islands; and on railway-cuttings the same phenomenon presents itself. In all these cases the seeds of the trees, or other plants which have sprung up when the soil was disturbed, were in most cases lying

---

[1] Ann. des Sc. Nat., 1824, ii. 270-284; and Recherches chimiques sur la végétation, 1804, chap. i.; Draper, Ann. Nat. Hist., 4th ser., xi. (1874) 45.

buried in the soil, out of reach of the necessary conditions of existence—though it must be remembered, also, that the wind may have wafted some of them from a distance [See PHYTO-GEOGRAPHY]. Seeds enveloped in wax have preserved their vitality for long periods, probably owing to oxygen having no access to the embryo.

It ought, however, to be mentioned, that the absolute necessity of seeds having access to air, in order to allow of the action of oxygen upon them, is not universally conceded by physiologists, since Edwards and Collin consider that the oxygen which combines with the carbon of the seed, and forms the CO_2 which is expelled in germination, is obtained, not necessarily from the air, but by the decomposition of water.[1] Becquerel and Boussingault[2] also consider that lactic acid is constantly formed during germination, and Edwards and Collin that acetic acid is formed during the same process, and that it is owing to the formation of this, and not to the formation of CO_2, that the carbon of seeds is lost—an opinion which we consider hardly tenable in the face of known facts.

4. *Light and Darkness.*—Contrary to the opinion of most botanists, and nearly all gardeners, it does not appear that light exercises any appreciable deleterious influence on germination,—Theodore de Saussure and Meyen having found that the seeds they experimented on vegetated in perfect darkness and daylight equally well; and these experiments the writer has repeated with much the same results.[3] The deleterious influence usually attributed to light may be owing to the unfavourable effect which light and heat exercise by drying the soil. In another experiment, Saussure caused seeds to be planted under two "cloches," or bell-jars, of equal capacity and under exactly similar circumstances; but one of these cloches was rendered opaque, while the other was left transparent. Under the transparent one the seeds germinated much more quickly than under the darkened one, showing that light exercises no deleterious influence, but probably a beneficial effect, by affording, as in this case, great heat without any subtraction of moisture to the seeds. Some plants, indeed—*e.g.*, heath and calceolarias—germinate better when uncovered by earth; and though seeds are buried in the soil away from light, yet many will germinate perfectly well if scattered on the surface, as they are naturally by the dehiscence of the fruits.

Hunt, and more recently M. P. Bert, in a report presented

[1] Comptes rendus, vii. 922; and Boussingault's Econ. rurale, i. 37.

[2] Ibid., vi. 102.

[3] See also Hoffmann's experiments (in Jahresbericht über Agrikultur Chemie, 1864, s. 110) with twenty-four kinds of agricultural seeds—the result of which was, that light exercised no appreciable influence on germination.

to the Academy of Sciences in 1871, have made some curious observations on the influence of the differently-coloured rays of light on germination. Hunt believed that the red rays are favourable to the process of germination, provided that moisture is supplied; but that the luminous rays, and those nearest yellow, have a most prejudicial effect on germination. Bert's observations were conducted more with a view to ascertain the effect of these different rays on vegetation than on germination; yet, as affording some remarkable results of the deepest importance, we present them here.[1]

On June 24, he sowed seeds of various plants, some of which prefer exposure to sunlight, others naturally growing in the shade, &c., under glass frames of various colours. On July 15, the plants requiring sun were all dead under the black and green glass, and were very sickly under the other colours, especially the red. The other plants were all declining. On August 2, all were dead under the blackened glass, except some seedling *Cactus*, *Lemna*, firs, and maiden-hair; under the green glass nothing was left alive but geraniums, celery, and house-leek, besides those that were not dead under the black: and all were in a bad state. The mortality was much less under the red glass, and still less under the yellow and the blue. The *Perillas*, which were killed outright under the black and green glass, lost their colour under the frames of other colours. The roots of some plants in pots were ascertained to be very slender under the black and green glass, in better condition under the yellow and blue glass, and well developed under the white glass. On August 20, the Acotyledons alone were still alive, though perishing, under the black and green; and as to the rest, the red had proved more hurtful to them than the yellow and blue. The stalks were much taller, but also less vigorous under the red than under the yellow and blue. Blue seemed to be the colour least detrimental to the plants; their greenness remained, and was even deeper than under the yellow. The plants under the white glass all continued to live, though less luxuriantly under dulled than under transparent glass. He concludes from his experiment that the green colour is nearly as prejudicial to plants as obscurity itself, a conclusion previously arrived at in the case of the Sensitive plant. Nevertheless, M. Bert says that plants very sensitive to light will turn towards the green rather than towards the red glass, and will direct themselves towards the latter in preference to the darkened glass.

---

[1] As reported editorially in the Gardeners' Chronicle, April 27, 1872, p. 569. See also p. 175 of the same volume. It is said that violet light has an extraordinary influence in hastening the growth of plants (Poey in Nature, 1872, p. 368).

The red colour is also very obnoxious to plants, though less so than the green rays. It causes them to become drawn in a singular manner. Yellow is much less injurious than green or red, but more so than the blue. In fact, each colour acting separately on plants is injurious more or less—the combination of all three in the proportions in which they are blended to form white light being essential to the perfect health of the plants; and, as a consequence, gardeners are recommended not to adopt the use of coloured glass for plant-houses and frames.

If, says M. Bert, the light which has passed through a leaf be examined by the spectroscope, it will be seen to be rich in green and red rays; hence it follows that these rays have not been turned to account by the plant, but have passed through it. It is therefore not surprising that plants cannot flourish if grown under the influence of light, of which, under ordinary circumstances, they make no use. To treat a plant thus is comparable to the attempt to feed an animal with its own excreta. The chlorophyll contained in different kinds of plants no doubt acts differently with regard to light, according to the particular kind of plant. Thus, while the underwood of an oak will not flourish beneath the shade of a large tree of the same kind, yet many ferns and mosses will thrive in such a situation, and various plants will grow well in the most shady places. Bert explains this, as before said, by the varying powers of utilising light which the leaves of the plants in question possess. Some points in these experiments are thus not in accordance with those of other investigators. The discrepancy probably arises from the varying intensities of the coloured glass, and perhaps from the different nature of the plants operated upon. At any rate, it is evident, Dr Masters considers—and most physicists will agree with him in this—that "we have not yet got to the whole truth of the matter."

The soil has, however, much influence on germination, in so far as it may be dry, moist, &c., owing to its physical composition, as we shall hereafter see.

Period of Time required for Germination.—The time required for the seed to remain in the soil before it will germinate varies from a few hours up to two years. The embryo of the mangrove (*Rhizophora*) sprouts even before the fruit has fallen off the branches into the soft marine ooze beneath.[1] The willow-seed will germinate in a few hours after being sown; the walnut or pine

---

[1] Others, such as the cucumber and melon, which are surrounded with pulp, may casually germinate while still attached to the plant. Wheat and other grains, every farmer familiarly knows, are apt to sprout when there is a long period of warm and rainy weather during their ripening, and the endosperm, from the partial transformation of its starch into sugar and dextrine, becomes sweet and glutinous.

takes from five to six weeks; while the rose, hawthorn, ash, dogwood (*Cornus*), beech, maple, *Pæonia*, and other trees—herbaceous in hard coverings—are said not to germinate until from one and a half to two years after being put into the ground. Cresses will germinate on the second day; onions a month after; acorns six months; while palms do not sprout until a year after being sown. Seeds out of the same pod, or off the same plant, will, however, take different times to germinate. For instance, M. Carrière found that seeds of a species of peach ("Pêcher Montigny") from the same tree germinated at different periods—an interval of four years elapsing between the time of the first and the last germinating. The same varying periods of germination have been noticed with lily-seed taken from the same pod. Again, it has been noticed that the period of time required for germination varies in accordance with the character of the seed—white, starchy, and thin-skinned, oily, or in thick envelopes; their rapidity of germination being in the order mentioned. Germination is quicker in some orders than in others—Grasses, Cruciferæ, Compositæ, Cucurbitaceæ, and some species of *Atriplex*, being the orders which spring most speedily after being sown. The age of the seed, the percentage of moisture, and the nature and chemical composition of the soil, as we have already discussed, have their influences on the time required for germination.

From the different methods taken to distinguish the periods of germination, it is not always easy to give satisfactory examples. Still we may consider that there are two periods of germination—viz.: 1. From the time at which the seed is put into the soil until the radicle appears; 2. Until the store of endosperm is consumed, and the plant set free to derive its nourishment from without.

From some observations made by Haberlandt, it appears that temperature had a considerable influence in hastening or retarding these periods of germination. At a temperature of 5° C. + (41° Fahr.), the rootlets of rye appeared in four days; those of other grains, clover, &c., in five to seven days; and in sugar-beet in twenty-two days, when the temperature was raised to 11° C. + (51°8 Fahr.) The time in the case of the seeds named was shortened one-half; while maize, kidney-beans, and tobacco germinated at this temperature in respectively eleven, eight, and thirty-one days.

Artificial Stimulants to Germination.—It is generally believed, though doubted both in theory and practice by some chemists, as originally announced by Alex. v. Humboldt, that weak chlorine-water accelerated the germination of seeds. This method is still occasionally used—especially in Continental gardens—to stimulate germination in old seeds. Göppert claims for bromine and iodine a similar influence; but there seems no truth in the assertion of Humboldt and others that various acids and salts (sulphuric, hydrochloric, phosphoric, and oxalic acids, salts of ammonia, &c.) have likewise the power of accelerating germination, the careful experiments of Hutstein leaving no doubt on this point; and equally untrue is it that alkalies have, on the other hand, a retarding influence on germination. The good effect of steeping seeds which it is desired to germinate speedily in urine, or causing them to be swallowed and voided by fowls (as in the case of hawthorn-seeds), as is still practised by farmers—it is said with success—is in all likelihood simply owing to the softening of the seeds by the imbibition of moisture during the process, and to no chemical action of the ingredients of the urine, or of those engaged in the process of digestion in the stomach and intestines. The observations of Nollet, Jallabert, Davy, and Becquerel, and particularly of the latter,[1] seem to show that electricity has a remarkable effect in hastening germination. Mustard-seeds subjected to the action of electricity germinated much more rapidly than others not under the same influence. The correctness of these observations has, however, been denied by various observers, chiefly agriculturists, and more particularly by Fyfe, who has attempted—not altogether with success—to demonstrate their erroneousness.[2] Cold and drought delay, but do not check germination altogether. Finally, as we have already seen, seeds buried deeply in the soil, out of reach of oxygen or the proper warmth necessary for germination, have their vitality dormant, but not dead. Lastly, as a general conclusion, it may be mentioned that the experiments of M. De Candolle at Geneva, and Senor Ramon de la Sagra at Havanna, on hundreds of species, proved that, as a rule—though there is the greatest variety in the times of germination in different species—the fresher the seeds, the shorter the time required for germination.

Proper Depth for Sowing Seeds. — Closely connected with, indeed intimately dependent on, the doctrines regarding the conditions necessary for the vitality of the seed and the process of germination, is the question, At what depth in the soil should such seeds be placed in order to germinate to the best purpose? Seeds are usually covered with soil more to keep them from the attacks of birds than really, as we have seen, from any *absolute necessity* of being so situated. Any one who has ever passed through a forest

---

[1] Archiv. de Botanique, i. 395.

[2] Trans. Soc. of Arts, iii. 109. For observations on the effects of electricity on vegetation in general, see,—Villari in Poggendorf's Ann., 1868, Bd. 1833, s. 425; Jürgensen in Studien des physiol. Instituts zu Breslau, 1861, Heft i., s. 38 *et seq.;* Heidenhein in Ebenda, 1863, Heft ii. 65; Brücke in Sitzungsber. der Wiener Akad., 1862, Bd. 46, s. 1; Max Schultze in Das Protoplasma der Rhizopoden (1863), s. 44; Kühne in Unters. über das Protoplasma, 1864, s. 96; Cohn in Jahresber. der Schles. Ges. f. vaterl. Cultur., 1861, Heft i. s. 24; Kabsch, Bot. Zeitung, 1861, s. 358; Reiss, Poggend. Ann., Bd. 69, s. 238; Buff, Ann. der Chemi und Pharmacie, 1854, Bd. 89, s. 80 *et seq.* (*teste* Sachs).

must have seen a number of plants sprouting without being in the soil, and only half covered with decayed leaves. Seeds, however, must be sown deep in dry porous soils, so as to enable them to obtain moisture. The Moqui Indians, of the Colorado desert, we are informed by Professor Newberry—and similar facts are within the author's own knowledge—plant their maize a foot or 14 inches in the soil, and raise excellent crops. The reason of this is, that the Colorado desert is excessively dry, and if the grain was planted in shallower furrows, no moisture would reach it, and it would not spring. To plant most seeds, in our climate at least, at such a depth, would be to insure them never germinating. R. Hoffmann[1] found that, out of twenty-four kinds of agricultural seeds, all perished when placed 12 inches below the soil (light loam); that at 10 inches, peas, vetches, beans, and maize alone came up; at 8 inches, in addition, wheat, millet, oats, barley, and colza came up; at 6 inches, in addition to those named, winter colza, buckwheat, and sugar-beet came up; at 4 inches all the above appeared, and, in addition, red and white clover, mustard, flax, horse-radish, hemp, and turnips; and at a depth of 3 inches, in addition to all those mentioned, lucerne made its appearance.[2] All difference in development, owing to earlier or later germination, disappeared before the plants blossomed. These conclusions of Hoffmann are not, however, borne out by the experiments of Grouven, who found, in trials with sugar-beet, that when the seeds were sown at a depth of ⅜ to 1¼ inch, such seeds gave the strongest and earliest plants; seeds deposited at a depth of 2½ inches required five days longer to come up than those planted at ⅜ inch. It was further shown that seeds sown shallow in a fine wet clay required four or five days longer to come up than those planted at the same depth in the ordinary soil.[3] The truth is, that all such experiments are modified by the nature of the soil, the supply of air and warmth, the kind of weather, the degree of moisture, &c.; and these are so variable that it would be rash to lay down any rule of practice which should not be received with the latitude which the circumstances mentioned would entitle it to.

Chemical Physiology of Germination.—The seed has germinated; the embryo is stimulated into life: now, how is it nourished and its growth kept up until it can extract its nutriment from the soil? At first the young plant lives entirely at the expense of the seed, feeding on the nutriment stored up in the endosperm, or, if

---

[1] Jahresbericht über Agrik. Chem., 1864, s. 112.

[2] Similar experiments were made by Petri, with the result, that while all of the seeds sown at a depth of 1 inch in the ground came up in twelve days, only one-eighth of those sown to the depth of 6 inches appeared in twenty-three days.

[3] Johnson, l. c., p. 303.

this is wanting, by the similar materials contained in its own cotyledons. This substance—viz., starch—is not, however, soluble in water; and as the nutrient material must be in a state of solution before it is fitted to nourish the embryo, this starch must be transformed into some substance which is soluble in water. The process involved in the nutrition of the seedling, therefore, falls under three heads—viz.:

1. The solution of the nutritive materials of the cotyledons or of the endosperm.
2. Their transfer to the embryo plant.
3. Their assimilation or conversion into the substance out of which the plant is built up.

1. *The Solution of the Nutritive Materials.*—The chemical composition of seeds varies very considerably, and accordingly the chemical process of solution is a much less simple one than might be at first sight imagined. The main *rationale* of the process is, however, not difficult to explain. In the case of *sugar*, *dextrine*, *gums*, *albumen*, and *casein*, there is not much difficulty, all these substances being capable of solution in water to the extent of one quarter to three times its weight. With *fats* our difficulties commence; for these, of course, are insoluble in water. Nevertheless, in seeds which are full of oil, nine-tenths of this disappears in the process of germination; while at the same time starch, and in some cases sugar, appears. Such, Sachs has shown, is the case with the squash. The oily seeds of the castor-oil plant (*Ricinus communis*), colza, sweet almond, in germination have their fatty matter converted into dextrine and sugar by the fixation of oxygen.[1] This starch undergoes a further change by being converted into dextrine and sugar—substances soluble in water. The insoluble albuminoids are gradually transformed into soluble modifications. Sachs even declares[2] that in the bean (*Phaseolus multiflorus*) "the starch of the cotyledons is dissolved, passes into the seedling, and reappears, at least in part, as soluble starch, without being converted into dextrine or sugar, as these substances do not appear in the cotyledons during any period of germination, except in small quantity near the joining of the seedling." We have seen (p. 213) that unorganised starch exists in the form of a jelly in various plants, such as in the seeds of colza and mustard. Arthur Gris, to add to our difficulty in forming a connected theory of the chemical process involved in germination, declares that after having completely deprived some seeds of "Indian shot" (*Canna*) of their endosperm, the cotyledons nevertheless replaced the starchy materials which they had not before germination, proving that, in this case at least, starch not only can

---

[1] Fleury in Adansonia, iv. 220-247 (*teste* Johnson, l. c., p. 304).

[2] Sitzungsberichte der Wiener Akad., Bd. xxxvii. s. 57.

be converted into sugar, but that sugar can reconvert itself into starch. These are, however, exceptional instances — the fact before mentioned being the rule in most cases, the nitrogenous substance known as "diastase" being the chief stimulating agent in such transformations. This diastase was discovered in 1833 by Payen and Persoz in the vicinity of the germinating embryo, but not in the radicle. They declare that one part of it is capable of transforming 2000 parts of starch first into dextrine and then into sugar, and that malt is composed to the extent of $\frac{1}{500}$th of its weight of this substance. It is, however, known, that any albuminoid in a state of alteration—in other words, as a "ferment"—may produce the same effect, though in a less marked degree than diastase. In the process they become decomposed and disappear. The processes involved can be best studied in the chemistry of malting,[1] which is simply that operation by which grain is made to germinate, and so converts the starch in it into sugar—after which, by means of artificial heat in a kiln, the germination is stopped.

Gaseous Products of Germination.—Carbon dioxide (CO_2) is evolved during the process of germination, and is probably due to the oxidation of the starch by the oxygen drawn from the air, though some observers have doubted this. The process Johnson illustrates as follows: Six molecules of starch absorb twelve atoms of O, and give rise to the production of five molecules of glucose or sugar of malt, together with six molecules of carbonic dioxide. The following equation represents such a change :—

$$6\ C_6H_{10}O_5 + 12\ O = 5\ C_6H_{12}O_6 + 6\ CO_2.$$

The correctness of this is, however, doubtful; and it is not improbable, as Johnson thinks, that the oxidation of the albuminoids of the seed gives rise to the disengagement of CO_2—and other causes may be at work. Among other gaseous products given off during germination may be mentioned carbonic oxide (CO), marsh gas (CH_4), ammonia (NH_3), and nitrogen (N).

Development of Heat during Germination.—Any one who has seen a heap of malt on a malting-floor must be aware of the great amount of heat developed during the process of germination. The heap of sprouting grain has to be continually turned over, lest the malt should be damaged by too much heat. The heat evolved is due to a chemical action going on—viz., to the absorption of water and oxygen, and also to the rearrangement of the proximate principles of the seed.

In a word, though germination consists of many processes, the main operation consists of : 1. The absorption of oxygen, the

---

[1] See an excellent account, by Dr Stein of Dresden, in Wilda's Centrablatt, 1860, Bd. ii. s. 8-23; or in Johnson's work, p. 304-307.

result of which is the disengagement of CO_2; 2. Starch is converted into dextrine, and that again into sugar; 3. Sugar is consumed and disappears, being converted into CO_2; 4. This combination is accompanied by the disengagement of heat.

Diminution of the Weight of the Seed during Germination.—Probably this may be accounted for by the disengagement of CO_2. Thomson and Boussingault have made some observations on this subject, but those of the latter observer are the most precise. One result may be quoted. He found that a grain of wheat which, when dry, weighed 2.439 gr., after germination did not weigh more than 2.365 gr., having thus lost 0.074 gr. in CO_2, &c. However, in 57 hours the same seed lost 57 per cent of its weight.[1]

2. *Transfer of the Nutriment to the Seedling.*—This is the second process in the nutrition of the young plant while yet dependent on the nutriment stored up in the seed. The water absorbed enters the cells, dissolves out the dextrine and sugar there stored, and carries it on to the embryo. The place where it enters the embryo is at the point where the cotyledons join the embryo; and hence the nutritive materials are "distributed at first chiefly downward into the extending radicles; after a little, downward and upward towards the extremities of the seedling." Sachs has observed that the carbo-hydrates (sugar and dextrine) occupy the cellular tissue of the bark and pith, while at first the albuminoids chiefly disperse themselves through the cambium layer, the first being full of air-passages, while the latter is destitute of them. He has also noticed that the albuminoids are present in greatest quantity at the end of the rootlets and of the plumule. Herbert Spencer considers that the nutriment from the cotyledons finds its way to the axis through the vascular tissue.[2]

3. *Assimilation of the Nutriment of the Seedling.*—Here we have a process exactly contrary to the first stage of nutrition—viz., instead of the nutritive materials being converted into *soluble* materials, they are converted by the plant into insoluble substances, such as cellulose. How this is accomplished we can at best only guess at. We see it done, but we cannot satisfactorily explain the intricately elaborate process. Possibly dextrine may be converted into cellulose, and the soluble albuminoids return to the insoluble condition in which they existed in the ripe seed (Johnson). At all events we find, according to Sachs, that the process of growth in the embryo consists of the enlargement of the ready-formed cells. In the process of growth, the starch contained in the cells disappears, and sugar is found in its place dissolved in the liquid contents of the cells. Examine the seedling again when

---

[1] Economie rurale, t. i. ch. ii. s. 1.

[2] Principles of Biology, ii. 543.

it has attained its full growth, and no sugar can be detected; while the walls of the cell, now enlarged and thickened, have accumulated cellulose.[1]

TERATOLOGY OF THE SEED.

Sometimes, either by the non-development of ovules, or by their abortion after being formed, no seed is produced.

Many plants, when treated as exotics, produce no fruit, and therefore no seed, or the fruit produced is destitute of seed (*e.g.*, *Musa*, *Arctocarpus*, &c.) Some of the cultivated varieties of the grape and the berberry produce no seeds. What is the precise cause of this is not well understood, but it is generally believed that excessive luxuriance of other portions of the plant, or an altered condition (such as when the carpels become foliaceous and their margins detached), tends to this. That hybridisation and cross-fertilisation have a tendency to diminish the number and size of the seed, we have already learned (p. 419). Seeds may also, as a teratological condition, be united in various degrees, either by their integuments or by their inner parts. This takes place in certain cultivated forms of cotton, which, from the seeds being aggregated in reniform masses, is called "kidney cotton." Union of the seed, which is, however, of rare occurrence, is termed *Synspermy* (Masters).

---

[1] The little which is known on these points may be found very clearly stated in Johnson's work, to which we have been indebted for many facts; in Sachs' writings quoted; and, more recently, in a memoir by M. Arthur Gris, crowned by the French Academy of Sciences in 1863. We have still much to learn on the subject, what we do know being only sufficient to point out our ignorance regarding nearly every portion of the subject. The following papers may also be referred to with advantage: Schröder in Jahrbuch f. Wiss. Botanik, vii. s. 261; Sorauser, Siewert, Roestell, and others, in Hoffmann and Peters' Jahresbericht über die Fortschritte der Agricultur chemie, 1868 and 1869; Sachs' Handbuche der Experimental Physiologie ("Stoffmet amorphosen"); and papers in Bot. Zeitung, 1859, 1862, 1863, 1864, and 1865; in Flora, 1862-63; Pringsheim's Jahrbuch, Bd. iii. s. 183 *et seq.;* Beyer in Landwirth. Veruchsstat., Bd. ix., &c.

CHAPTER XIII.

GRAFTING: LONGEVITY OF PLANTS, ETC.

FLOWERING-PLANTS are in general reproduced from the seed, which may, in some respects, be looked upon as a modified bud, the ovule being, as we have seen, only a bud produced on the edge of a leaf—viz., on the placenta. Plants can, however, be propagated by buds alone, just as we do in planting "cuttings" in the ground. These cuttings send forth adventitious roots, while the bud or buds in them continue the plant in an upward and onward direction. Again, an exactly similar operation is performed in planting potatoes. The slice of potato is simply a shoot identical with the cutting from an aerial stem, only that in this case the cutting is from a tuber or underground stem, and the "eye" or bud is placed under the soil, speedily sending up an aerial stem to produce the flower and fruit, though the edible portion remains underground in the form of the arrested underground stem or tuber (p. 103). There is another method of propagating plants from buds, which is known in horticulture as *grafting*. Though this has only a secondary connection with botany, we may briefly state the general principles connected with the operation. It consists in uniting one plant or portion of a plant to another, either by means of a bud or a budding branch transferred to the other. The one united is called the *graft*, while the plant to which it is united is known as the *stock*.

This may be accomplished in three ways :—

1. A bud may be removed, along with a piece of bark of the graft, and transferred to the stock, with the tissues of which the tissues of the portion of the graft transferred unites.

2. A piece of a branch of the graft, with one or more buds, may be transferred to a place prepared for it on the stock, and then, as in the former case, bound firmly to the stock, and protected from the weather, when the corresponding tissues of stock and graft will unite. In fact, both of the foregoing cases are just like planting cuttings in a new soil—the soil in the present case, however, being the wood of the stock; and the means through which

the graft nourishes itself by the juice of the stock is not by roots sent into the stock, but by the union of the tissues allowing of a continuity of the nutritious channels from stock to graft.

3. By binding the branches of two trees or shrubs together—both being rooted in their own soil; and after they have united, allowing them either to remain or to sever the connection. In this manner quaint ornamental hedges are sometimes formed.[1] It is technically known as *inarching*, or "grafting by approach," and is sometimes seen naturally performed by forest-trees.[2]

It is probable that all of these methods of grafting were known to, and practised by, the ancients—at all events, the Greeks and Romans were acquainted with grafting, although they often associated the wildest ideas in connection with it. It is, however, only within the last two hundred years that the art has been practised either extensively or on scientific principles.

Advantages of Grafting.—Grafting preserves accidental varieties, which could not be kept "true" by being propagated by seed. If the seeds of apples are sown, they have all a tendency to revert to the original crab. But by means of grafting, some accidental good variety, which has been produced on some particular branch, can be perpetuated. In this way the almost endless varieties of our pears and apples have been propagated. Several varieties can also be produced on one bush or tree; and by this method our gardens are enriched with double-flowered plants, such as all the numerous varieties of roses, camellias, &c., which could not otherwise be kept up from year to year.

---

[1] Described in Hunter's edition of Evelyn's Sylva, i. 141. See also Mr James M'Nab in Trans. Bot. Soc., x. 452.

[2] The following, which we have from a correspondent, is an illustration of another peculiarity in trees uniting naturally: "In the pretty village-green of Lynchmere, Sussex, there is a row of old pollard-oaks. We were struck by observing a birch-tree growing in close contact with one of these oaks. On examination, we found that the birch was growing from the lowest fork in the oak, and that below that point the trunk of the oak was completely split, and the birch pushing its roots in the shape of arms right down the hollow of the decayed oak to a point within a yard of the ground. On another of this row of oaks was a mountain-ash, small, but thriving; but this birch-tree, encased in its oaken covering, was a much more striking phenomenon.—On the bank of a side stream of the Cherwell, at Oxford, there stood, a few years ago (and probably does so still), a pollard-willow, on the top of which a sycamore had grown. The root of the sycamore had run down the hollow trunk of the willow, and seemed to be gradually becoming converted into a trunk itself; for the old willow's natural tendency to split was being increased by the strong growth of the sycamore. It would be curious if, as seemed likely to occur, the sycamore eventually were to stand rooted in the ground, after the decay of the willow, with some five-feet of original root transformed into trunk." This is, however, not a case of inarching, as the wood of the two trees does not seem to be united.

Most horticulturists are agreed that grafting enlarges and improves the fruit, though the idea entertained by others—Duhamel Rozier, &c.—that by continually grafting grafts upon grafts (or, as they style it, *greffe sur greffe* or *contregreffe*), fruit might be indefinitely "ennobled," is not borne out by known facts. The graft has often earlier flowers after grafting than before, especially if grafted on an old stock; but in general it has little or no effect on the stock. It is said, however, that there are a few exceptions to this rule on record—such as the statement by Jussieu and others, that grafting a spotted-leafed variety of *Abutilon* upon a uniformly coloured leafed stock, in course of time altered the leaves of the stock to the character of those of the graft, and that this alteration continued even after the graft was removed. Morren, however, looks upon this as a case of contagious disease.[1] Gardeners also affirm, that when the pear is grafted on the quince and medlar, the fruit is smaller and more highly coloured than when "worked on" a pear stock; and that if grafted on the mountain-ash (*Pyrus aucuparia*) it is earlier in flowering. The most extraordinary fact (?) regarding the influence of the stock on the graft is given in a recent contribution by Signor Zenone Zen to the Royal Institute of Venice, who declares that after long study and experiment he has succeeded in producing varieties of roses by budding, the flowers of these varieties being very different from those of the plants from which the buds were taken; and M. Dubreuil has also made a similar statement,—neither observer having, however, as yet given details sufficient to allow us to judge of the correctness of these assertions.[2] Again, if a quicker-growing plant is grafted on a slower-growing one, the graft grows as rapidly as before; but in this rapidity of growth the stock does not share.[3] Lastly, it ought to be mentioned that instances are not wanting where grafts became so modified in their growth as to in no way resemble the parent plant.[4]

Physiological Conditions necessary to Grafting.—The first of these is, that the graft and stock must be closely allied—species belonging to different natural orders, or even to families not closely connected, wanting the necessary physiological conditions to allow of grafting together. They may appear to grow, but there is no union, the graft only subsisting for a time by means of the juices which it may abstract from the stock, with which it is in mechanical connection. The chemical processes in the two plants are not similar, and therefore they will not unite. To do so, each tissue must be placed in direct contact with the corre-

---

[1] The maxim often laid down that variegation and double flowers never go together, is not, however, altogether irrefragable, a wallflower having been seen with both monstrosities (Morren in Belgique Horticole, April and May 1870).

[2] Revue Horticole, cited in Gardeners' Chronicle, 1873, p. 104, 117.

[3] Lindley's Theory of Horticulture, p. 23.

[4] Ibid., 22.

sponding tissue in the other plant—cambium to cambium, albumen to albumen,—and so on. To give a few examples, you can graft all the different varieties of the rose upon one another. All the species of the same genus, or in some cases even the genera of the order, are capable of being grafted together. The apple can be grafted on the peach, apricot, prunes, almonds, &c., because all these plants belong to the same order (Rosaceæ). Nevertheless, there are some singular exceptions. For instance, so closely allied are the pear and apple, that Linnæus put them into one genus (Pyrus). Yet it is with great difficulty that the one can be grafted on the other; and the graft does not easily grow, and bears no fruit for one or two years, finally perishing: while, on the contrary, the medlar (*Mespilus Germanica*) can be grafted with the utmost ease on the hawthorn (*Cratægus oxyacantha*), which, though both belong to the Rosaceæ, are by no means so closely allied as the pear and apple. You cannot, however, graft the rose on the holly, or the vine on the walnut, &c., as the ancients imagined—these plants belonging all to different orders.[1] It has been supposed that some particular orders, such as Coniferæ, cannot be grafted; but this is an error. Among Coniferæ, however, grafting is not so easily done as among most other plants—species generally of the same genus, or at least very closely allied, only being capable of forming an organic union with one another.

After the graft and the stock have united, the characters of the wood of the two plants are never lost; and if a section is made through them, the line of demarcation can be distinctly seen. Finally, it may be stated that there is no ground for the hypothesis of Knight, that the life of a graft is only equal to the life of the plant it had been taken from.[2]

The description of the various modes of grafting practised under the three general heads mentioned, in no way belongs to scientific botany; it is a part of the operations of horticulture, and therefore calls for no extended account in this place.

LONGEVITY OF PLANTS.

Plants, we have seen, may be arranged, in accordance with their duration of life as individuals, into *annual*, *biennial*, and *perennial* (p. 294), though this can be altered by preventing flowering, or otherwise changing the conditions of life, as already explained (p. 296). In general language, it may be said that the

---

[1] The only apparent exceptions to this general law are the mistletoe and other plants of its order (Loranthaceæ), which will bear grafting on trees of other orders, such as the apple, oak, &c. As this is a natural parasite, it cannot, however, be looked upon as a true exception to the law mentioned.

[2] A Selection from Horticultural Papers, p. 80.

plant dies whenever it can no longer reproduce itself. A perennial plant is one to whose term of existence there is no determinate limit. This being so, the question arises, The conditions of existence not being rudely disturbed, how long can a plant live without dying of natural decay? or, Has every individual a determinate limit of existence, longer or shorter, like individual animals? The *species*, geology shows, has a certain limit of existence; and in time it disappears, to give place to another form, gradually and lineally, most likely, descended from itself by the operation of certain natural laws. The *individual* has, we may be certain, also a limit to its existence, though that limit varies according to the species of plant and its nature, but being in all cases much shorter than the duration of the *species*.

The age of woody plants is determined by means of the annual "rings," each ring being usually believed to represent a year's growth. We have, however, seen (p. 88), that this test is not infallible, some tropical trees showing almost no division into rings, the distinction between the growing and the dormant season being so slight; while in trees of northern climates, a "cold snap" in the midst of a warm growing season will divide the annual layer of wood into what would be considered to be two layers, and therefore be accounted as two years' growth. However, in most cases the rings afford a tolerably accurate series of data to go upon in estimating the age of trees. Care should, however, be taken to count the rings; or if an average is taken from measuring the diameter of the stem, that this diameter should be estimated not simply by doubling *the half* of the stem—for frequently the thickness of the growths of the annual rings of wood is much greater at one side than at the other.[1]

Some trees attain an enormous size. The great banyan-tree (*Ficus indica*) of India is said by tradition to be the same tree which sheltered under its umbrageous foliage Alexander the Great and 10,000 men. It has 350 large and 3000 smaller stems, and, whatever may be said of the historical tradition connected with it, must be of great age. Some Brazilian Hymeneas are 84 feet in circumference at the butt. The *Adansonia digitata*, or Baobab tree,[2] is said to be more than 5000 years old. It is among Coni-

---

[1] In the Museum of the Californian Academy of Sciences, San Francisco, is a fir log from Puget Sound, in the centre of which is a bullet surrounded by 160 rings of wood. Not a trace of a passage through which the bullet entered can be seen; and accordingly, if a zone of wood forms in every tree every year in Puget Sound (Washington Territory), then it must have been 160 years since this bullet was embedded in the fir log. However, as Puget Sound has only been trod by the first white man about 60 years ago, and it is not 80 yet since Vancouver sailed up it and a bullet was known in that region, there is an awkward difficulty in the affair whichever way we turn, physiologically or historically.

[2] Adanson, Familles des Plants, preface, ccxv.

fers, however, that some of the largest and oldest trees are found. Scotch firs, larches, &c., often attain the age of 200 years; cypresses 500; and De Candolle[1] thinks that yews attain even a greater age. At Crowhurst, in Kent, was one which was estimated to be 1458 years old; at Fountains Abbey, in Yorkshire, another was, in 1770, considered to be 1214 years old; a third, in the churchyard of Fotheringham, in Scotland, measured 58 feet 6 inches in circumference, and from the number of annual zones of wood, was believed to be 2588 years old; while a fourth, in the churchyard of Brayburn, in Kent, was reported by Evelyn in 1660 to have 2880 rings.[2] At Peronne, in Picardy, there is—or was until recently—a yew known to have been flourishing in A.D. 634; and another, at Staines, was, in 1830, 9 feet 3 inches in diameter at 3 feet from the ground, and the extent of its branches embraces a circle of 207 feet.

Some specimens of *Taxodium distichum* attain in Florida a circumference of 40 feet. In Vancouver Island, I have measured a *Thuja gigantea*[3] 45 feet in circumference at the butt, and close by it an *Abies Menziesii* 28 feet in circumference 2 feet from the ground. In the garden of Chapultepec, in Mexico, the "cypress of Montezuma" (*Cupressus disticha*) attains a circumference of 41 feet; while another, near Santa Maria de Tesla, in the province of Oaxaca, exceeds 117 French feet. All of these measurements are dwarfed, however, by the enormous *Sequoia* (Wellingtonia) *gigantea* of California, one specimen of which must have attained a circumference of 112 feet, and is considered, from the annual rings, to be upwards of 6000 years old—an estimate the accuracy of which has been doubted by Mr De la Rue, who considers it not more than 1234 years old, estimating each ring as an annual one.[4] The stump is now smoothed, and a house erected over it, where dancing-parties are held by visitors, the butt of this enormous tree affording room for a moderate-sized ball-room! Few of the standing trees in any of the Wellingtonia groves date beyond the Christian era. Some specimens of *Sequoia sempervirens* which I measured in Northern California were not greatly inferior in size to their gigantic congener. In Australia some of the *Eucalyptus* trees attain, it is said, even a greater size.

The proportion between the height and thickness of Conifers varies from 1.35 to 1.120, showing a different ratio to that which prevails among other orders of Dicotyledons.

---

[1] Physiologie Végétale, ii. 1001.

[2] Zuccarini, Ray. Soc. Reports, 1846, p. 21.

[3] Monograph of the coniferous genus *Thuja*, L., &c., Trans. Bot. Soc. Edin., vol. ix.

[4] Gardeners' Chronicle, Nov. 6, 1858; Jackson, Proc. California Acad. of Sciences, 1867; Proc. Bot. Congress in London, 1866; Asa Gray, Ann. Nat. Hist., 4th ser., xi. 52; Kronise's California, 506, &c.

On Olivet are eight olive-trees which are known to have existed prior to the capture of Jerusalem by the Turks.

In the garden of the Duc d'Aremberg, at Brussels, is a linden-tree which, according to the records of the city, is more than 700 years old. In the Canton of the Grissons there was, in 1798, a linden which measured 51 feet in circumference, and is recorded to have existed in the fifteenth century. Many huge and aged oaks still exist; and numerous other instances, showing to what great age trees may attain, might be quoted, but the above will suffice. Here is a tabular view of the ascertained ages of some trees belonging to different natural orders, compiled by Moquin-Tandon for his 'Tératologie Végétale:'—

Years.
Palms, 200, 300.
Cerios, 300.
Chirodendron, 327.
Elm, 355.
Cypress, 388.
Ivy, 448.
Maple, 516.
Larch, 263, 576.
Chestnut, 360, 626.
Citrus (orange, lemon, &c.), 400, 509, 640.

Years.
Platanus (plane), 720.
Cedrus, 200, 800.
Walnut, 900.
Tilia (lime), 364, 530, 800, 825, 1076.
Abies (fir), 1200.
Quercus (oak), 600, 800, 860, 1000, 1600.
Olive, 700, 1000, 2000.
Schubertia, 3000, 4000.
Leguminosæ, 2052, 4104.
Dracæna, 6000.

The Death of the Plant.—The plant simply consists of the individual organs, or collection of organs, which go to make up, either by their bulk or their formation, the life of the plant. You cannot style all the cuttings taken from a plant, and which in their turn grow into plants, as part of it. Link's[1] dictum that the "seed continues the species and the bud the individual," is only correct in a limited, and certainly not in a literal sense. "I cannot conceive," writes Schleiden, "of the Creator as a journalist who issues his works leaf by leaf in continuation. Science regards a tree as an aggregate of many individuals—a kind of polyp-stock; life, proceeding upon another distinctive character, calls it an individual: but neither science nor life as one-thousandth of an individual. I imagine that any person of sound mind would smile if any one were to regard the 2000 poplars of a German *chaussée* a mile in length as a continuous individual; and still less would it be admitted that a one-year-old span-long shoot of a weeping-willow was essentially a continuation of an old individual, who, in his rapid departure from the East, left his youth lying on the borders of the Euphrates, where long ago it died and was decomposed, whilst its commencing manhood was cherished by Alexander Pope, and many years since was hewn down

---

[1] Elem. Phil. Bot., ed. 2, i. 133.

and cast into the fire." Yet all the weeping-willows in Europe sprang from a twig, which formed part of a wicker-basket, which was sent from Smyrna to the poet Pope, and which he planted, as it showed signs of life. The true interpretation of the words would be, that buds originate individuals which frequently resemble the parent plant in more characters than those which originate from the seed. Yet, according to Lindley, these "water-shoots" (individuals developed from buds) are frequently distinguished from the parent by an enormous development of leaves. Shoots of the oak, springing from a felled branch, are often found in woods with leaves a foot long. A "simple plant," Schleiden—to whom we are indebted for nearly all our "philosophy" on this subject—defines as one which does not produce axillary buds so as to develop into branches; or if it does produce axillary buds, these are exclusively developed into flowers. Most of these are, however, so exhausted with the reproductive effort, as to die after producing their seed,—so that his physiological definition of a simple plant is, one "only capable of propagating once; with the unfolding of its terminal bud into reproductive organs, its life is closed." With annual and biennial plants this is the case; hence the name of *Monocarpiæ* which De Candolle applied to them. "Sometimes they continue to live, and the terminal bud goes on developing, and is capable of producing new reproductive organs, as in *Ananas*. In compound plants the same takes place with the single individuals of which they are composed. In this case a very remarkable condition sometimes occurs; the seeds of many perennial plants, originating themselves from seed, are entirely incapable of reproducing the individual, and this power of producing reproductive organs is first possessed by buds produced from individuals in the tenth or new generation." In reality we must look upon a plant as a compound individual, just as a Sertu-

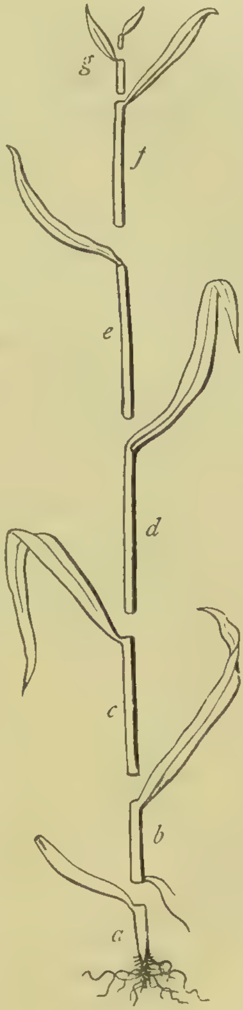


Fig. 353.—Diagram of a simple-stemmed plant like a grass, and of the similar parts or phytons, *a* to *g*, of which it is composed.

larian zoophyte is a compound animal made up of many polypes upon a common polypidum—though to carry the analogy between the zoophyte and the animal much further, as has been done, is only to wander into a region of dreamy mysticism, where wordy guesses take the place of facts. In the accompanying diagram (fig. 353), copied from one of Gray's, this idea has been attempted to be carried out. Perhaps it is only just to express the author's idea in his own words.

"A simple stem bears nothing but leaves in some form or other, and its branches are only repetitions of itself, following the same laws. The embryo consists of a primary joint of stem covered with a bud, the first leaves or leaf of which takes the form of *cotyledons;* and the following ones develop as ordinary foliage, and leaf after leaf, or pair after pair, is formed and elevated upon the successive internodes as the stem is built up. At the close of the growing season, if the stem is to endure, this is terminated, as it began, by a bud; and the bud-scales, if any, are developed in this peculiar form, subservient to protection alone, and borne upon nodes which are never separated by elongation of the internodes. With the ensuing spring growth commences, and another set of internodes, and of nodes bearing ordinary leaves, form the second year's growth, like the first; and so, by annual increments, a simple leafy stem is developed and carried up. Not only is the whole stem, growing from year to year, thus composed of a succession of similar growths, each the offspring of the preceding and the parent of the next, but also each annual growth itself consists of a lineal succession of similar parts—viz., of leaf-bearing joints of stem, developed each upon its predecessors, and in turn surmounted by the next in the series. These *similar parts*, which by their repetition make up the phanogamous plant, have been termed *phytons*,[1] or plant elements. The first phyton is the radicle of the embryo, with its cotyledon or pair of cotyledons expanding its leaf or pairs of leaves, and then giving both to the next phyton, or joint of stem and leaf,—and so on in lineal succession. So that the whole herb, shrub, or tree, as to its upward growth, is a multiplication of the simple plantlet it began with as developed from the seed. Moreover, any joint of stem, when favourably situated for the purpose, may produce secondary roots, and thus complete the vegetable individuality, having all the organs of vegetation. The repetition of these similar parts in the direct line, and each from the summit of its predecessor, builds up a simple or main stem, to which many plants are restricted during the first year's growth, and some, such as palms and reeds,

---

[1] By Gaudichaud, from the Greek φυτόν, a plant. He talked about three merithals or parts—viz., the *radicular* (corresponding to the root), *cauline* (to the stem), and *foliar* merithals (corresponding to the leaf).

throughout their whole existence. These productions from new starting-points give rise to branches."

Any of these phytons may die, but yet the connecting-links between them—*i.e.*, the stem and root—may live so far, just as some polypes in a hydrozoon may die, while the others may live. However, when any of these polypes cease for a time, from injury, or altogether by death, to contribute their share to the general life of the compound individual, then the first stage towards the death of the compound individual has commenced. Otherwise there is no determinate conclusion to the life of the plant. Unless it met, as it usually does, with some mechanical injury, it might live on for ever.

We have now concluded the biography of the plant, looking on it as an individual, and as a flowering, *Phanerogamous* or *Phænogamous* plant alone. In the last chapter, we have seen that there are two main modes of reproduction in such plants—viz., 1. by seeds; 2. by buds. There is still another mode of reproduction—one more simple in some respects, and more complicated in others—and that is, by the simple cell. Such a mode of reproduction is only found in the flowerless plants, or *Cryptogamia;* and as this mode of reproduction is connected with various modifications of all the other organs, it is better to devote a Section to these plants solely, when considered from a systematic point of view, rather than mix up the description of their mode of life with that of the flowering-plants, which they differ so widely from.

SECTION IV.

GENERAL PHENOMENA CONNECTED WITH PLANT-LIFE.

In the preceding Sections we have successively examined the organs of flowering-plants which are subservient to the nutrition and reproduction of the individual. There still remains for consideration a number of phenomena connected with plant-life which cannot be well classified under any of the preceding heads, or those which are to follow. These, though not directly connected with one another—and, indeed, in many cases entirely distinct, and more closely allied to some of the former sections—it has been usual in systematic text-books to throw together in one special section. Perhaps though from a strictly scientific point of view this may be open to animadversion, still experience has shown that it is useful from a didactic point of view. Accordingly, at this stage the student is called upon to consider various interesting phenomena of vegetable biology, which may be classified as follow: 1. Mimicry of plants. 2. Free movement of plants. 3. Spontaneous or automatic movements of plants. 4. Special directions of root, stem, &c. 5. Opening and closing of flowers. 6. The sleep of plants. 7. Vegetable irritability. 8. Movements of climbing plants. 9. Odours of plants. 10. Colours of plants. 11. Luminosity of plants. 12. Temperature of plants. 13. Vegetable nosology. All of these questions are of the deepest philosophical interest, and several are for the first time presented to the English student in a systematic form.

CHAPTER I.

HOMOPLASMY: MOVEMENTS AND SPECIAL DIRECTIONS IN PLANTS.

OF late years attention has been called, chiefly by Bates and Wallace, to the remarkable resemblances which exist between certain species in the animal kingdom, particularly insects, and between the animals and the trees and ground which they inhabit, such resemblances being apparently to protect the species in the "struggle for existence." Not only do these insects emulate other insects of orders less attacked by birds, but, as in the case of *Phasmata* or *Mantides*, dry sticks and leaves, even to the veining of the leaves; and even simulate the attacks of parasitic fungi, droppings of birds, and larvæ; and there are spiders which imitate the axillary buds of plants. Something similar exists in plants. Professor Thisleton-Dyer, who has paid much attention to it,[1] considers that in all large natural families of plants there is a more or less distinctly observable general habit or *facies* easily recognisable by the practised botanist, but not always as easily expressed in words. He considers that what have hitherto been called *mimetic* plants are simply cases where a plant belonging to one family puts on the habit characteristic of another. *Mutisia speciosa*, a composite plant from Western South America, has a scandent leguminous habit closely agreeing with that of *Lathyrus maritimus* of the European shores. In the same way, three different genera of ferns have species (found in distant parts of the world) undistinguishable in a barren state. Plants with willow-like leaves frequent the borders of streams in certain countries. In every natural order there are plants which might at first sight be mistaken as belonging to some other order—as *Bupleurum* in the Umbelliferæ as belonging to the Euphorbiaceæ, &c. Schultz (Bipontinus) remarks that in Compositæ alone the habit of almost every other tribe might be detected; and *Stangeria paradoxa*, a Cycad (fig. 342), was absolutely described by Kunze as a true fern. The *Equiseta*, or horse-tails, have their echoes in the

---

[1] Brit. Assoc. Rep., 1871, Sections, p. 128; and Nature, 1871, p. 507.

Hippuris, which is a flowering-plant; and the New Zealand *Veronica tetragona* is so like a coniferous plant, that it was doubtfully figured by Sir William Hooker as *Podocarpus Dieffenbachii*. *Scarocyphala Gerrardi* of the Cape is so like another twining leafless Asclepiad—*Sarcostemna viminale*—that, except by its flowers, the latter is with difficulty distinguishable. These instances may be multiplied to almost any extent. We will have occasion to mention the resemblance in odours of different orders, and the same likeness might be pointed out in other points.[1] To this, Thisleton-Dyer applies the term *Homoplasmy*, and considers that the cause of the phenomenon is, that the influence of similar external circumstances moulds plants into the similar form most advantageous to them. Different external conditions may, however, produce the same result; in this respect they may be called analogous. He considers that there is no true mimicry in the vegetable kingdom, such as is found in the animal; but though this may be so in some cases, there can, we think, be little doubt that among plants there are true cases of "mimicry." In plants, however, unlike Lepidoptera, there seems no protective benefit to be derived from it, and in neither case is there any *conscious* effort at convergence. Cases of homoplasmy in plants are referable to two distinct classes—resemblances in general habit, and resemblances of particular organs. The former, as in the case of the homoplasmy between a *Cactus* and a *Euphorbia* or a *Stapelia*, or between a *Kleinia* and a *Cotyledon*, are no doubt due to the operation of similar external conditions of climate and soil; but in the second class this explanation of Professor Thisleton-Dyer's fails. In the *Ophrys apifera*, or bee-orchid, there is what might be thought a case of protective resemblance, the flower being so fashioned as to attract bees to assist in its fertilisation. But, on the contrary, the bee-orchid is one of the few plants of its order that appears to be perpetually self-fertilised, never being visited by insects. The carrion-like odour of the *Stapelia* may, however, act as a benefit to the plant by attracting bluebottle and other flies to assist in its fertilisation. It has also been pointed out that the rare Scottish *Menziesia cœrulea* may have been protected "from the rapacity of botanists" by the common *Empetrum nigrum*, which grows abundantly beside it, having been mistaken for it. "Biologists generally are probably hardly prepared to apply the terms *intelligence* and *will* to the vegetable kingdom; but the use of the term "vegetable life" seems to me to imply of necessity that there are powers at work in the economy of the plant, as well as of the animal, which it is in vain to attempt to reduce to manifestations of the forces which govern the inorganic world."[2]

---

[1] See Grindon's 'Echoes in Plant and Flower Life' for a long series of these.

[2] A. W. Bennett in Nature, Nov. 2, 1871; Pop. Sc. Review, Jan. 1872;

FREE MOVEMENT OF PLANTS.

When we come to consider the fructification of the Algæ, we will see that the spores of most of the lower species, when first discharged, swim about freely in the water, exactly like some of the lower animals, and that these free movements only cease when the spore begins to germinate. Hence they are called "zoospores" (fig. 354). These movements are caused by the vibration of minute cilia on the surface of the organism. The corpuscles or spiral filaments of the antheridia of most of the cryptogamia also exhibit movements (figs. 355, 356). All of these movements can be enfeebled or arrested by the application of chloroform, or of a weak solution of opium or other soporific.

Fig. 354.—Zoospore of *Vaucheria Ungeri*, Th., composed of a single cell.

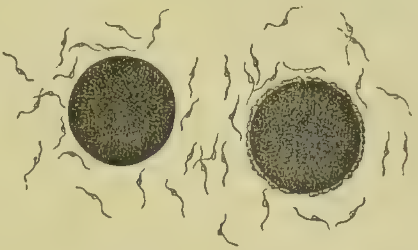


Fig. 355.—Fecundation of the bladder-wrack (*Fucus vesiculosus*), showing free-moving "spermatozoids" about the spores.

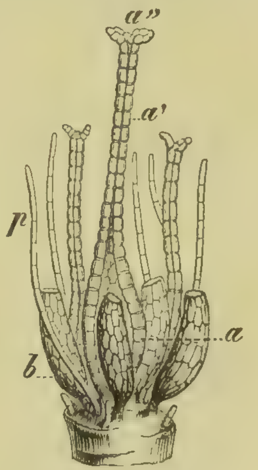


Fig. 356.—Group of the "archegonia" (*a a' a"*) and "antheridia" (*b*), mixed with the "paraphysia" (*p*) of a moss (*Bryum bimum*).

Though the higher Algæ in their adult state are fixed, yet the lower ones are often free during the whole of their existence, so that for long their vegetable character was a matter of doubt. Of this description are many of the Desmidiaceæ and Diatomaceæ, Oscillatoria, &c.—all very minute plants; and though they execute motions from place to place more or less rapidly, the cause of the motion is still a subject for future discovery.

---

and Britten in Field Quart. Mag. and Rev., ii. 313-316; also Bates in Naturalist on the Amazon, and in his Memoir on the Lepidoptera of the Amazon Valley in Linn. Trans., vol. xxiii.; Wallace, Contrib. to the Theory of Nat. Selections (Essay on Mimicry); A. Murray in Nature, 1870, p. 155; and various other notes and letters in the same volume by different writers.

SPONTANEOUS OR AUTOMATIC MOVEMENTS OF PLANTS.

There are certain other movements displayed by the leaves of plants which do not appear to be affected by external agents in the same way as others, which we will presently describe in Mimosa, Dionæa, &c., but equally strange and inexplicable.

Hedysarum.—In the Presidency of Bengal grows wild a plant described by Linnæus as *Hedysarum gyrans* (Desmodium gyrans, DC.), which, since it was first known to exhibit the peculiar property which has given it its specific name, through the observations of Lady Monson, has been the subject of numerous researches by Broussonet, Pohl, Linnæus the younger, Sylvestre, Hallé, Cels, and others, and a complete work by Hufeland.[1]

The plant belongs to the order Leguminosæ, and the leaves are compound-uniconjugate, imparipinnate (fig. 357), the two lateral ones being very small compared with the terminal, which is from 3 to 4 inches in length. Both the lateral and the terminal leaves move, but the movements of the two are different in their character. The large leaf is very sensible to the influence of light and darkness; and the general petiole participating in the movement, the position of the leaf is entirely changed during day and night. Gradually, as the sun lowers, the leaf lowers itself, until at night its under surface is applied against the stem. Beyond this diurnal gyration it has no motion, or at least moves too slowly to be seen, though at times it has been observed to move somewhat actively. Very different is it with the two lateral leaflets, which are continually jerking up and down, until they come in contact with, or even cross each other above and then below, the petiole, unaffected by day or night so long as the temperature is sufficiently elevated—thus being even more automatic than the first-mentioned case. The motion of the leaflets will sometimes stop in some portion of their accord, and then suddenly, without apparent cause, will commence again. It cannot be set in motion by a touch. Exposure to cold, or cold water poured on, will stop the motion; but if the

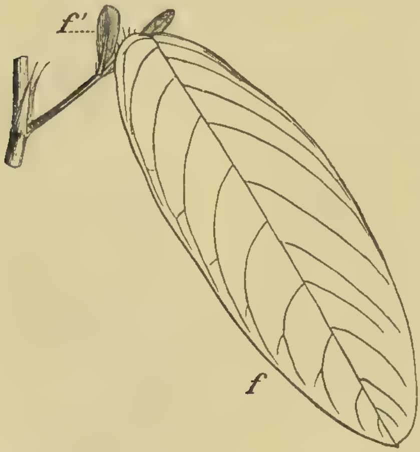


Fig. 357.—Leaf of *Hedysarum gyrans*, L. ("pinnately trifoliate"), with the odd leaflet, *f*, incomparably larger than the two lateral ones, *f'*.

---

[1] It was introduced into this country by Dr Russel in the year 1775.

plant is again subjected to the influence of warmth, the motion will recommence. If it is temporarily stopped by the leaflets being held, they will immediately resume motion after the restraint is removed; and for a short period, as if making up for lost time, will move with increased velocity: gradually, however, they will resume their former speed. The cause of this motion is perfectly unknown, though it is easily seen that it consists in a simple flexion of the petiole proper of the leaflets. Electricity, according to Hufeland, has no effect whatever on it. Even the stem is sensitive to the influence of the sun. It is of the nature of a rhythmical motion, such as is seen in the vacuoles of zoospores, or in the bands of protoplasm with which the zoospores are connected, only $\frac{1}{9000}$th of an inch in diameter, in *Volvox globator*—an alga "which contracts with regular rhythm, at intervals of from 38 to 41 seconds, quickly contracting, and then slowly dilating again."[1] Though the movements described are most familiarly known as seen in *H. gyrans*, it is said that they are also apparent in *H. vespertilionis*, Linn. fil., of Cochin China, and, according to Nuttall,[2] in *H. cuspidatum*, W., of the Southern United States; but in regard to the last-named species, as well as *H. gyroides* and *H. lævigatum*, showing the movement, there is considerable doubt. Dutrochet is also said to have observed analogous movements in the leaves of the pea and haricot bean.

Labellum of Orchids—Megaclinum, &c.—In several tropical orchids, especially in a species of *Megaclinum* (*M. falcatum*), and *Pterostylis*, the lower petal or labellum exercises somewhat spontaneous movements, consisting of a raising and depression of the labellum at intervals of a few minutes, but "with great freedom and pertinacity."[3] Another orchid (*Drakea elastica*) shows irritability in the stalk of the labellum. In several species of the genus *Bolbophyllum*, this irritability of the labellum has been recorded as noticed; and Dr Hooker[4] mentions that the labellum of the Australian genus *Calæna* is so irritable, that when an insect alights on it, it suddenly shuts up against the column, and "encloses its prey, as it were, in a box"—an action probably favourable in some way to the fertilisation of the plant. These movements, however, not being automatic, ought properly to come under the head of irritability, as might also the closing of

---

[1] Busk in Trans. Mic. Soc. London, 21st May 1852. Similar movements, at intervals of 40 to 45 seconds, were afterwards observed by Cohn in the vacuoles of *Gonium pectorale*, and in *Chlamydomonas*—Untersuch. über die Entwickelungsgeschichte der Mikrosk. Algen. und Pilze, 1854.

[2] Gen. of North Am. Plants, ii. 110.

[3] First observed by Lindley, but most minutely described by Morren (Ann. des Sc. Nat., 2e sér., xix. 91).

[4] Flora of Tasmania, ii. 17.

the petals of *Gentiana sedifolia* (a plant belonging to another order) when touched.

The Compass Plant.—The "compass" plants (*Silphium laciniatum*) of the Western American prairies[1] present their edges north and south, while their faces are turned east and west, the leaves on the developed stems of the flowering-plants taking rather an intermediate position between their normal arrangement on the stem and their peculiar meridional position. The settlers, when lost on the prairies in a dark night, get their bearings by feeling the direction of the leaves. The reason of this is, that both sides of the leaf are equally sensitive to light. In *Silphium laciniatum* 20 stomata were found on either side; and in other species, the numbers, though not equal, were yet far from being so unequally distributed as in most plants (p. 56). From this it follows that the two sides will seek an equal exposure to the light, the mean position of equal exposure in northern latitudes being that in which the edges are presented north and south, the latter to the maximum, the former to the minimum, of illumination.[2]

Return of Leaves.—Somewhat analogous to the foregoing is the return of leaves to their natural position when this is artificially interfered with. Leaves, we have seen, in their normal condition, have two aspects,—an upper, looking towards the sky; and an under, facing the earth. If the leaf is gently twisted round, so that this position is reversed, and held in this constrained position for some time, it will return again to its normal one on being released. This is accomplished by means of the petiole, and chiefly the inferior end of this organ. Age and the consistency of the tissue, and the differences in hue and structure between the two sides, have considerable influence over the power of the leaf to accomplish this automatic motion. The leaves of some plants are so mobile that they will follow the course of the sun. In young plants it is accomplished much more quickly than in old plants; and in plants whose tissues are indurated, it is with great difficulty that it can be done. Under the influence of bright sunlight it is also accomplished more quickly than in darkness. Finally, if the experiment is tried frequently on the same leaf, the return is accomplished more slowly each time. In a vine-leaf experimented on by Bonnet, after the first and second time it returned to its natural position in the course of one day,

---

[1] It is found from Texas on the south to Iowa on the north, and from Southern Michigan on the east to 300 or 400 miles west of Missouri and Arkansas.

[2] W. F. Whitney in American Naturalist, 1871, p. 1-3; see also General Alvoid in Proc. Ann. Scientif. Assoc., second meeting; Gray in ibid.; Hill in Amer. Nat., iv. 495; Gorrie, Trans. Bot. Soc. Edin., 1860, &c.

while it took four days after the fourth, and eight after the sixth experiment. This movement, as in the "sleep of plants," is facilitated by the articulation of the leaf to the stem, and the unequal "tension or turgescence of the cells on both sides."

Heliotropic Plants.—That the peduncle of certain plants will twist round in the course of the day, so as to bring the flower continually exposed to the sun, and back again in a contrary direction next morning, was well known to the ancients. In the Roman mythology, Clytie,[1] inconsolable for the loss of the affections of Sol, follows him wherever he goes under the form of a flower called *Heliotropium*. What the exact species of this plant is, has not been ascertained;[2] but what the ancients fabled is, we know, really accomplished in well-known plants—*e.g.*, various Compositæ, including, it is said, the sun-flower (hence, probably, its name), the phenomenon described being known as the "nutation" of such plants. The ripe ears of corn, heavy with grain, also scarcely ever incline to the north, but always to the south. The cause is not clearly ascertained.[3]

Movements of Leaves of Colocasia esculentea.—Of late, M. Lecoq has recorded some remarkable movements, of a spasmodic character, in the leaves of *Colocasia esculentea*, quite different from those in the Sensitive plant, but occurring spontaneously, independently of the action of the wind or any external cause, at irregular intervals, and at different periods of the day or night. Sometimes the quivering motion affecting the whole plant is sufficient to tinkle little bells attached to the branches, and on one occasion even to shake the pot in which the plant was contained, and to resist a pressure of the hand, the number of the pulsations varying from 100 to 120 per minute. M. Lecoq states that *Colocasia* is destitute of stomata, and he attributes the phenomenon to the incessant pulsations of the imprisoned sap.[4]

Movements of Leaves in Water.—The leaves of *Schinus molle* (Nat. Ord. Anacardiaceæ) thrown into water have a peculiar jerking motion. The same is observed in the leaves of other plants of this order. Small sections of leaves of the "poison-oak" (*Rhus Toxicodendron*) leap about in the water, though not with the same force as those of *Schinus molle*. It is also said

---

[1] "Mad Clytie, whose head is turned by the sun."

[2] It cannot be the *Heliotropium* of the moderns, because Ovid (Met., lib. iv. 250) describes it as resembling the violet; nor can it be the sun-flower, for this plant is a native of America, and could not, therefore, be known to the Roman poet.

[3] For remarks on transversal geotropism and heliotropism in plants, see Franks, Bot. Zeit., 1872.

[4] Belgique Horticole, quoted by Bennett in Nature, 1869, p. 142; *vide* also Pop. Sc. Rev., vol. xi.

that the same phenomenon may be occasionally witnessed in the leaves of *Rhus aromatica*, *R. glabra*, *R. Copallina*, and *R. typhina*.[1] So far as we have examined this curious and little-known subject, the jerking motion of the leaf-sections seem to be hygroscopic—*i. e.*, caused by the imbibition of water into the parenchyma.

SPECIAL DIRECTIONS OF ROOT, STEM, ETC.

Allied to automatic motions must be classed the special directions of different parts of the plant—especially the unerring course by which, under normal conditions of life, the root will direct itself downwards and the stem upwards. Even the mistletoe will send down its roots into a tree in the same fashion as other plants do in the earth. If a plant is grown in complete darkness, still the stem will ascend and the root descend. And, as if showing that it is not the substance into which they grow that is the governing cause of this, if a germinating seed of the mistletoe is laid in contact with a cannon-ball or other hard substance, from which, of course, it can derive no nourishment, it will still direct its roots downward and towards the circumference of the ball.

Most ingenious attempts have been made by various physiologists[2] to account for this, and almost every force of nature, from gravitation upwards, has been summoned to the aid of the theorists; but as yet we are far from possessing clear ideas on the subject. That light has a great effect on the upward and downward movements of the stem and root, is certain from the fact that the plant grown in a dark closet to which light is only admitted by a small aperture—the keyhole, for instance—will direct itself towards that aperture. Schultz and Mohl also managed, by growing seeds on damp moss, so arranged that the only light which they could receive was from below, to cause the root to ascend and the stem to descend. Most probably these special directions are some of the ultimate facts of nature which we may observe, but yet never be able to explain. Still, recent researches seem to show that, so far as light is concerned in causing stems and branches to direct themselves towards the light, it is the refrangible rays of the solar spectrum (viz., blue, indigo, and

---

[1] Meehan in American Naturalist, 1871, p. 689.

[2] Dodart, Knight, De Candolle, Erasmus Darwin, Henry Johnson, Dutrochet, Duchartre, Poiteau, and Kielmeyer, and others. Nearly every one of these botanists has broached a different theory, which for a time held sway among a narrower or wider circle of disciples; but each, one after the other, has gone down before the irresistible force of facts.

violet) which produce this singular action; for if a seed is germinated on a piece of cotton-wool floating in a glass vessel of water in an apartment lighted by a yellow, orange, or red light, the stem, while ascending, will show no tendency to seek the light, nor the root to curve itself to that side of the vessel from which the least light comes.

CHAPTER II.

OPENING AND CLOSING OF FLOWERS: SLEEP OF PLANTS.

It has long been known that certain plants open at certain hours of the day and shut at others. The ancients, as related by Theophrastes and Pliny, believed that the "lotus of the Euphrates" disappeared beneath the waters of the river at night, and rose to welcome the sun in the morning.[1]

The illustrious Linnæus was, however, the first who paid scientific attention to the subject, and his observations form to-day the basis of all our knowledge regarding this department of botany. By watching the time of opening of different flowers, Linnæus and other botanists have constructed what they have somewhat fancifully called a "Floral Clock." The times of the opening and closing of flowers vary, however, according to locality,[2] and are hardly so punctual to a few minutes as the lists in such floral clocks would lead us to believe. The following may be taken as examples of about the time certain plants open: Bindweed (*Convolvulus sepium*) about 3 A.M.; goat's-beard (*Tragopogon pratense*), 4 A.M.; poppy (*Papaver nudicaule*), 5 A.M.; *Convolvulus tricolor*, 6 A.M.; white water-lily (*Nymphæa alba*), 7 A.M.; pimpernel (*Anagallis arvensis*), 8 A.M.; marigold (*Calendula arvensis*), 9 A.M.; *Mesembryanthemum glaciale*, 10 A.M.; Star of Bethlehem (*Ornithogalum umbellatum*), 11 A.M.; purslane (*Portulaca oleracea*), mid-day; *Scilla pomeridiana*, 2 P.M.; *Mirabilis jalapa*, 5

---

[1] From the time of Sir J. E. Smith up to the present date, the assertion has been frequently made that the flowers of the white water-lily, *Nymphæa alba*, sink beneath the water at night to rise in the morning — a supposed fact alluded to in some well-known lines by Thomas Moore. After repeated observation of water-lilies in all climates, I am convinced that this is an erroneous statement. The *Nymphæa* in question does certainly close its flowers after dark, and open them under the stimulus of the sunlight, but does not immerse them in the water. It is said that some tropical water-lilies will partially open their flowers under the influence of moonlight (T. Britten in Field Quart. Mag., iii. 46).

[2] There is, for instance, about one hour's difference between the time of opening of the same flowers at Paris and at Upsal.

P.M.; *Silene noctiflora*, 6 P.M.; while *Cereus grandiflorus*, *Cooperia*, *Convolvulus purpureus*, and others, do not open until after dark. Between all these hours there are, both as to closing and opening, intermediate members of this "floral clock." Some flowers (like most orchids) after the flower once expands, remain open until it fades; others,[1] like flax (*Linum usitatissimum*), close a few hours after expanding, never to open again; while others (as in the examples given as a specimen of the floral clock) open and close at regular hours until the flower dies away. The time during which flowers remain open also varies. For instance, the white water-lily will remain open for twelve hours, while the purslane closes in about an hour after it opens at mid-day.

Hygrometric Plants.—The tender constitutions of plants seem also to be affected by changes in the air of which we are not sensible; hence changes in the weather can be presaged from observations of certain plants closing up. If the Siberian sow-thistle (*Sonchus Sibericus*) shuts at night, it is said that the ensuing day will be fine; and if it opens, it will be cloudy and rainy. If the "African" marigold (a Peruvian species of *Tagetes*) shuts after seven o'clock in the morning, rain is near at hand. If *Convolvulus arvensis* (bindweed), *Calendula pluvialis* (marigold), or *Anagallis arvensis* (pimpernel), are already open, they will shut at the approach of rain; hence the last, from this susceptibility, has earned the title of the "poor man's weather-glass." The *leaves* of *Porleria hygrometrica* are also hygrometric, folding down or rising in accordance with the state of the atmosphere.

Different Periods of Flowering.—Every species of plant has a different season for flowering—a fact so familiar to us that we are apt to lose sight of the inexplicable character or reason of this. Hence we have spring, summer, autumn, and winter flowering plants. The *Daphne mezereum* of our shrubberies is, for instance, covered with flowers in February; the buds of primroses are not expanded until March or April; the lilac (*Syringa vulgaris*) and the horse-chestnut do not flower until May; *Colchicum autumnale* not until late in the autumn; while *Helleborus niger* flowers in December. Some plants, again, only flower for a short time, *Draba verna*, *Veronica verna*, peaches, almonds, apricots, hyacinths, &c.—*e.g.*, for a short time in early spring or summer; while the fetid Hellebore (*Helleborus fœtidus*), the shepherd's-purse (*Capsella Bursa-pastoris*), the dahlia (*Dahlia variabilis*), and whin (*Ulex*), are covered with blossoms from spring to early winter, and even in the case of the latter plant through the winter also. It has been observed that plants in which the flower-buds are formed the preceding autumn, and wait for the spring warmth to expand them, are in general short-flowered; while, on the other

---

[1] Called by Linnæus "ephemeral flowers."

hand, those plants which develop and mature their buds the same year are covered with flowers for a lengthened period. It is very doubtful if light is the sole agent in the opening or shutting of flowers. Heat seems to have a greater influence. If plants are removed from a warmer to a colder climate, the plants expand at a later hour in the latter. A flower which opens at six o'clock in the morning at Senegal, will not open in France or England till eight or nine o'clock, nor in Sweden until ten o'clock. Again, a flower which opens at ten o'clock at Senegal, will not open in France or England till noon or later, and in Sweden will not open at all; and, finally, a flower which does not open until noon or later at Senegal, will not open at all in France or England. The same is true regarding the period of flowering. The almond, which flowers at Smyrna in the early part of February, flowers in middle Germany in the second week of April, but not in Christiania until the beginning of June. Plants transferred from the northern hemisphere will, after the first year they arrive in the antipodes, flower in winter—the season corresponding in time to the summer of their native land—but soon they will accommodate themselves to the altered seasons. Cases now and then occur in which a particular individual will flower before or after the usual time of species to which it belongs—as, for instance, a horse-chestnut mentioned by De Candolle, which always flowered a month before others in the neighbourhood of Geneva. Such idiosyncrasies are propagable by the horticulturist's art.[1]

THE SLEEP OF PLANTS.

The opening and closing of flowers may be described as the sleep and wakening of these organs, but the term is more usually applied to the folding of the leaflets of certain plants during night. The student, however, ought to be warned that it has nothing in common with the sleep of animals—there being no flaccidity in the plant whatever—the leaves, though in another position to what they were during the day, being quite as rigid as during that period. The phenomenon is well seen in the foliage of most leguminous plants, of those of the wood-sorrel (oxalis),[2] and exceedingly well in the leaflets of compound plants like the false acacia, *Cassia floribunda*, &c. The subject has been investigated by Valerius Corda in 1581, and even earlier by Garcias de Horto in 1567; but it is to Linnæus and De Candolle that we are indebted for the most precise observations regarding the different positions

---

[1] Fritsch, Proc. Imp. Acad. Sc. Vienna, lxiv.

[2] Morren in Bulletin de l'Acad. Roy. de Bruxelles, t. iv. v. vi. and xii.

the leaves assume at night. From the observations of the two latter botanists, the following table is compiled :—

SIMPLE LEAVES.	*Face to Face* (folia conniventia), opposite leaves raised up so as to touch each other by their superior face. Ex. *Atriplex.*
	Enveloping (f. includentia), alternate leaves, raised up so as to envelop the stem. Ex. *Sida.*
	Funnel-shaped (f. circumsepentia), differs from the preceding in so far that their superior portion surrounds the stem in a funnel-shaped form. *Ex.* Peruvian mallow.
	Protecting (f. munientia), falling down. Ex. *Impatiens noli tangere.*
COMPOSITE TRIFOLIATE LEAVES.	*Cradle-shaped* (f. involventia), leaves turned back, and meeting so as to touch each other by the summit only. Ex. *Trifolium incarnatum.*
	Divergent (f. divergentia), turned back and diverging from their superior surface. *Ex.* Melilota.
	Pendent (f. dependentia), hanging down, so as to touch by their inferior surface. Ex. *Oxalis.*
COMPOUND PINNATE LEAVES.	*Straight up* (f. conduplicantia), leaflets turned upwards above the common petiole, so as to touch by their superior surfaces. *Ex.* Colutea.
	Turned down (f. invertentia), turned down, so as to touch by their inferior surfaces. *Ex.* Cassia.
	Imbricated (f. imbricantia), leaflets imbricated along the common petiole *almost* to the summit. Ex. *Mimosa.*
	Retrorse (f. retrorsa), leaves imbricated along the petiole almost to *the base.* *Ex.* (unique) *Tephrosia caribæa.*

Equally with the special directions, the sleep of plants has been the subject of many explanatory theories; but as none of these are satisfactory, or will bear the test of close examination, the student will lose nothing by being led past the troubled waters of such controversies. Stirring up exploded hypotheses is proverbially an idle task. Suffice it to say that Bonnet, Hills, De Candolle, Mustel, Hoffman, Ratchinsky, Sachs, and others, have all figured as the authors of rival theories. The nocturnal position, though different in different species, is always uniform in the same species. This shows that the displacement of the leaves is not mechanical. Again, it can be proved not to be a passive state; for in the honey locust-tree the leaflets are turned upwards, and in the Sensitive plant forward and upward—a position they would not assume it they fell by their own weight. De Candolle found that most plants could be made to acknowledge an artificial night and day, by illuminating the room they were in at night by lamps, and darkening during the day, and that the sensibility to light resided in the petiole and not in the blade, as the movements continued when nearly all of the latter portion was cut away. He found, however, as in the Sensitive plant, that after a time they got used to the darkness, and expanded and contracted their leaves for a time, though at uncertain intervals. The movements of the leaflets are, however, not altogether dependent on light. For instance, the Sensitive plant (*Mimosa pudica*) begins its "sleep" just before sunset, but its waking frequently precedes the sunrise. There is also little, if any, connection between the closing of the flowers and the sleep of the leaflets in the plants where both of these phenomena occur. On the authority of Bertholot, we learn that an *Acacia* in Teneriffe regularly closes its leaflets at sunset and unfolds at sunrise, while its flowers close at sunrise and unfold at sunset. In regard to the *force* with which the plants close their leaves, Dassen found, by experiments with the leaves of the garden-bean, that the mean force exerted by the leaflets of that plant in being raised to their nocturnal position was equal to three grains.

CHAPTER III.

VEGETABLE IRRITABILITY, AND MOVEMENTS OF CLIMBING PLANTS.

THERE are some movements of plants which, unlike those already described, are not altogether automatic, but are influenced by touch or other mechanical causes, and are said—for want of a better name—to be due to vegetable irritability. Let us note a few of the more common instances of this.

Mimosa.—Perhaps in no plants is this irritability better shown than in some Leguminosæ, especially in Mimosas, or Sensitive plants. These plants have bipinnate leaves, with four secondary petioles starting from a common rachis or petiole, each of the petioles being provided with a number of pairs of leaflets, which are expanded horizontally during daylight. If the common Sensitive plant (*Mimosa pudica*) is suddenly jarred or touched, the leaflets will change their position, overlapping one another from below upwards, close to the secondary petiole; on greater irritation being applied, the secondary petioles also bend forward and approach one another, and finally the general petiole sinks down, by means of a bending at its articulation or junction with the stem. If they

Fig. 358.—Bipinnate leaf of Sensitive plant (*Mimosa pudica*).

are moved by the wind, they will move altogether. If the stem is cut, no injury ensues to the sensitiveness of the plant. After the plant has been the subject of experiment for a consecutive number of times, it seems to get used to it, expands its leaflets again, and acts very sluggishly. The temperature of the air has also an effect on it—a sudden change either to hot or cold destroying for the time being its irritability. In our hothouses it is also rarely so sensitive as in its native climate. There the concussion caused by a horse galloping along the road on the sides of which the plant grows, will often have the effect of causing the leaves to fold up. We have often noticed this effect produced by the passing of a train along the Panama railroad in New Grenada, on the sides of which the plant grows abundantly. So sensitive are they, that on one plant folding its leaflet, the contact will irritate its neighbour, and so on—the irritability travelling along the patch almost as fast as the traveller can keep up with it in walking. If the plant is irritated by means of rays of the sun concentrated by a lens, or by caustic substances applied to the terminal leaflets or pinnæ, the irritation will be communicated to the neighbouring ones, one after another, until the whole plant is affected by it—this result in general following in the space of four or five minutes, according to the size or vigour of the plant (fig. 358). It may also be mentioned that, contrary to the assertion of Runge, there is no difference in this respect in the action of acrid or alkaline caustics. It displays the irritability best when in a moist warm atmosphere, one of 75° or 76° Fahr. being the most favourable for it. Electricity, if applied by shocks at intervals, has the effect of causing the leaves to fold in the manner already described; but if a continuous current is applied, it seems to have no influence on the movement, its effect being merely that of any other mechanical irritant. Bert has recently shown[1] that plants of *M. pudica* died in the dark in twelve days, having lost all sensibility at the seventh. In green light they died in sixteen days, sensibility being gone at the twelfth. In violet light the plants perished at the end of three months without having increased in development, but sensitiveness remained to the end. In blue light they continued to live without development, but with a certain degree of sensibility. The plant loses its sensitiveness under the influence of chloroform and ether,[2] and, as if capable of accustoming itself to any irritation, it will by-and-by, if carried in a carriage for a distance, open the leaves it at first shut before it had accommodated itself to the jolting (Desfontaines).

The causes of these movements are not so well made out. It is, however, known that the movements are propagated through the

---

[1] Comptes rendus (1870), t. lxx.

[2] Masters, Nature, 1870, p. 343.

fibro-vascular bundles alone. Meyen,[1] Brücke,[2] and Sachs,[3] have all studied the anatomical structure of these plants with a view to determine this matter. At the base of the common petiole, and as well at the secondary ones, are swellings which are concerned in causing the raising of the leaves when the irritation communicated along the fibro-vascular bundles, by a peculiar arrangement of these bundles around the periphery of the swellings, as described by the authors named, reaches them. This movement is probably accomplished, according to Sachs, by a movement of the liquid contents of the cells composing these swellings.[4] It may also be noted that it is a common subject of observation, that if the lower surface of these swellings, at the base of the common petioles, is touched, instantly the leaf is depressed; but no such effect follows if the *upper* portion is subject to irritation. The opposite is the case if the swelling at the base of the leaflets is the subject of experiment. Again, it has been found that if the leaflets at the extremity of a secondary petiole are touched, the folding of the leaves consequent on the irritation is continued from above downwards; but if a pair at or near the base is touched, the contrary ensues—viz., the irritation is conveyed from base to apex.

Dionæa.—Near Wilmington, in the State of North Carolina, U.S., is found a very curious plant, often called "Venus' fly-trap"[5] (*Dionæa muscipula*). Every leaf (fig. 359) of this plant bears at its sumit an appendage which is probably the true blade, while what seems the leaf is only an expanded winged petiole.[6] A midrib divides this appendage into two equal parts, on the upper surface of which are three or four hairs, and along their margins are also rows of long, closely-set hairs. On an insect alighting on the leaf, the

---

[1] Pflanz-Physiologie, iii. s. 532 *et seq.*

[2] Müller's Archiv. für. Anat. u. Phys., &c., 1848, ss. 434-455.

[3] Bot. Zeit., 1857, col. 793-802, 809-815, pl. xii. and xiii.; and Handbuche der Experimental-Physiologie der Pflanzen, s. 481. See also Dutrochet, Recherches Anat. et Physiol. sur la structure intime des Animaux et Végétaux, 1844.

[4] Pettigrew considers that the cells of these swellings constitute, as it were, two springs, which act in opposite directions, "so that if from any cause the one be paralysed, the other pushes the leaf in the direction of least resistance." These "springs" are set in motion, he thinks, by the rush of fluid creating a turgid state of the one set of cells and an empty state of the other. Moisture, being necessary to the life of the plant, cannot act as an irritant. "The only explanation that can be given is, that the plant lives, and that it sucks in moisture by the one set of cells, and ejects moisture by the other."—Lectures on the Circulation, l c., p. 99.

[5] Though in its mechanism it acts much more like a rat-trap.

[6] Meyen, on the contrary, looks upon the inferior portion as the true leaf, and the terminal contractile portion only as a sort of appendage; while Dassen has hazarded the opinion that the two lobes of this latter part are only the remains of distinct rudimentary leaflets.

two sides close along the line of the midrib, the marginal bristles dovetailing into one another like the teeth of a rat-trap, so that the insect is crushed to death, and the harder it struggles to escape the firmer it is clasped. The leaf then remains closed until the insect is dead, when it opens for another capture, though in time it acts sluggishly, and by-and-by becomes insensible. The leaf performs this movement equally well in daylight or dark, and the younger leaves possess a much higher irritability than the old ones. What is the purpose of this we are yet in ignorance. The old ideas of Ellis and Curtis, though generally discredited until recently, that the plant feeds on the insect remains, are not quite so undeniable as might be supposed. Recently some remarkable observations go far to prove that the face of the blade is thickly scattered with glands which secrete a saliva-like liquid. In the course of a week or two this liquid acts as a sort of gastric juice, and dissolves all the soft parts of the insect. Little pieces of raw beef were acted on in the same way ; so that really here we have a carnivorous plant ! When it is mentioned that these observations were made by, among others, Asa Gray and Charles Darwin (though those of the latter botanist are as yet unpublished), the reader will consider that he has a strong guarantee that the facts stated are correct. The observations of Knight, made many years ago, were to the same purpose—viz., that those leaves supplied with bits of raw beef were more flourishing than those not so supplied. Finally, we have Dr Burdon-Sanderson announcing[1] that the closing of the leaf of *Dionæa* in the manner described, is accompanied with electrical phenomena analogous in their nature to

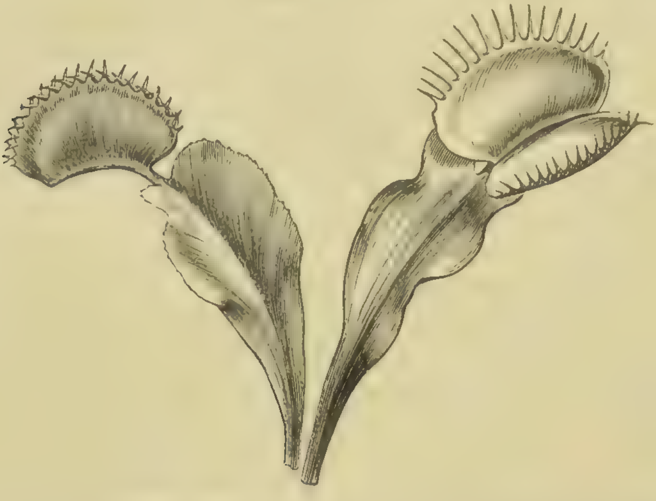


Fig. 359.—Leaves of *Dionæa muscipula*, L., closed and open (almost the natural size).

---

[1] At the meeting of the British Association at Bradford, Sept. 20, 1873.

those which occur when nervous or muscular actions are induced in animals.

Drosera.—The leaves of the "sun-dews" of our bogs (*Drosera rotundifolia*, *D. media*, and *D. longifolia*), which are covered with glandular hairs (p. 61), have been proved to be also sensitive, though in a much smaller degree than those of the plants described in the foregoing paragraphs. These glandular hairs, each secreting a drop of glutinous fluid, attract insects to their destruction. Each hair has a spiral within it, and when a fly alights on the limb of the leaf on which they are placed, all the parts of the limb, as well as the hairs, move towards that part, the result of which is, that the insect is smothered by means of the viscid fluid which they secrete—a remark made by Roth nearly a century ago. Mr A. W. Bennett, who has recently made careful observations on this subject, observed that it was not until the insect was dead that the hairs bent over the dead fly—a fact not easily accounted for by the supposition of the presence of a "contractile tissue" at the base of the glands. To quote the *ipsissima verba* of the description which he gives us of his experiments on *D. rotundifolia:* "The contact of the insect appeared to excite a stronger flow of the secretion, which soon enveloped the body ot the animal in a dense and almost transparent slime, firmly gluing down the wings and rendering escape hopeless. It still, however, continued its struggles, a motion of the legs being clearly perceptible after the lapse of three hours. During all this time the insect was sinking lower and lower down among the glands towards the surface of the leaf, but only a trifling change had taken place in the position of the glands themselves, which had slightly converged so as to imprison it more completely. But after the struggles of the prisoner had practically ceased, a remarkable change took place in the leaf. Almost the whole of the glands on its surface and its margin, even those removed from the body of the insect by a distance of at least double its own length, began to bend over and point the knobs at their extremities towards it, though it was not observed that this was accompanied by any increased flow of the secretion from them. The experiment was made in the evening, and by the next morning almost every gland of the leaf was pointing towards the object in the centre, forming a dense mass over it. The sides of the leaf had also slightly curved forwards, so as to render the leaf itself more concave."

Though this irritability has been denied, the researches of numerous observers, particularly of the botanist just quoted (many of whose observations I am also enabled fully to confirm), and of Nitschke, have quite proved this, at least in reference to *D. rotundifolia*, in which it is shown that all portions of the leaves are irritable, but that this power chiefly resides in the hairs, and that the leaf is irritable in proportion to the activity of these glandular hairs. After the hairs have covered over the insect like the fingers of the hand, they do not straighten for some days, when a fresh drop is exuded for a fresh prey. This secretion is acrid and bitter to the taste, and is sufficiently acrid to cause irritation if applied to the skin.[1] In a recent note presented to the French Academy of Science,[2] M. Ziegler has made some curious observations on this subject. He found "that all albuminoid animal substances, if held for a moment between the fingers, acquired the property of making the hairs of *Drosera* contract; though, if such substances had been in contact with a living animal, no such action was visible on the hairs. The cause of this is obscure. After a time the hairs get insensible to insects, or to organic bodies modified by living contact." The properties of these plants were reversed, and, strange to say, their hairs were found to contract under the influence of organic matter which had been previously in contact with packets (of double or triple envelopes) containing sulphate of quinine. Organic matter, influenced in this purely physical way by sulphate of quinine, has no contractile action on the hairs of *Drosera* in their normal state. The plants whose physical properties had been reversed by the influence of albumen (animal albumen was used), could be restored to their normal condition by placing them for twenty-four hours, with the platinum capsules containing them, on a packet of sulphate of quinine. The method may be adopted whenever, from any cause, the leaves have become insensible to insects. In every case the contraction of the hairs is slow; it commences visibly, and is not complete till after several hours. In all our experiments, and those of Mr Bennet, the contact of a minute chip of wood, or other dead matter, had no effect on the movements of the hairs or leaf. In some cases the insect is merely fastened to the leaf, and in time dies of starvation; but in other species with stronger hairs, the insect is really secured by the bending inward of the hairs, so as to bring it within reach of the glutinous drops, though the movement is so slow as not to be visible except in the result. In *D. longifolia*, it has been affirmed, the limb of the leaf not only shows an inclination, as in *D. rotundifolia*, to curve, but actually "incurves itself so as to fold round its victim." Linnæus long ago observed that the flowers of *D. rotundifolia* in Sweden opened at nine o'clock and shut at noon; but whether this has any connection with the peculiar irritability of the leaves is very dubious.

---

[1] It has been used in the treatment of dropsy, intermittent fever, and ophthalmia, but without effect. The superstition of many countries invested it with a virtue of supplying suppleness to the limbs if applied to them.

[2] May 6, 1872 (Comptes rendus, t. lxxiv. 1227-29).

The whole subject will bear reinvestigation.[1] It has even been affirmed that, as in *Dionæa*, the frond has the power of digesting the flies![2] Lastly, Treat has confirmed most of the above observations on *Drosera filiformis*, but with the additional observation, that when living flies are pinned at a distance of half an inch from the apex of the leaf, the leaf actually bends towards the insect until the glands reach it and suck its juices![3]

Other Plants with Irritable Leaves.—In addition to the plants named, there are others which show sensibility of the same kind, though not in the same degree. Among these may be enumerated various other species of *Mimosa* (above all, *M. sensitiva*, and, in a less marked degree, *M. viva*, *M. casta*, *M. speciosa*, *M. asperata*, &c.) Among other Leguminosæ showing sensibility, are *Acacia julibrissin* of Turkey, *Smithia sensitiva* of India, *Æschynomene sensitiva* of the West Indies and Brazil, *Æ. Indica* and *Æ. pumila*, both of India, *Desmanthus stolonifer* of Senegal, &c. Outside of the order Leguminosæ, the most remarkable sensitive plant is *Biophytum sensitivum*, DC. (*Oxalis sensitiva*, L.)—a small plant of India, which in its native country has a sensibility almost equal to that of the Mimosa, though in our hothouses it is much less sensitive—*Averrhoa Carambola* of Bengal, &c. The frond of *Onoclea sensibilis*, a fern, will, if touched, bend downwards. If the ordinary butterwort (*Pinguicula vulgaris*) is rudely torn up, the flower-stalk immediately begins to curve back-

---

[1] I have, in accordance with universal custom, both here and in former pages, designated the peculiar glandular appendages of *Drosera* as "hairs." Trecul and Grönland, I am aware, have, however, denied that they are true hairs—though this is simply a question of difference of definition as to what a hair is—but integral portions of the substance of the leaf penetrated by a fibro-vascular bundle with spiral vessels (in other words, by a vein). Be this as it may—and all physiologists are not at one on the subject—the student will find these hair-like structures (or "trichome," as the Germans call them) in *Drosera* investigated with great care by Meyen, Uber die Secretions-organe der Pflanzen, s. 51, tab. vi., fig. 15; and Pflanzen physiologie, ii. s. 478; Grönland, Ann. des Sc. Nat., ser. 4, t. iii.; Trecul, ibid., iv. 3; Nitscke, Bot. Zeit., No. 22; Ibid., No. 33 (1860); Caspary, ibid., No. 26; Martinet, Ann. des Sc. Nat., ser. 5, xiv. (1872) 195-198; Hanstein, Bot. Zeit., 1868; Rauter, Zur Entwickelungsgeschichte einiger Trichomgebilde (1871); and most recently of all, by Warming in Videnskab. Meddel. fra den naturhisk. Forening i Kjöbenhavn, No. 10-12, 1872, p. 159-202, where the "trichomes" or hair-like structures of the petals of *Menyanthes trifoliata*, *Gunnera scabra*, *Datura Stramonium*, *Drosera rotundifolia*, *Agrimonia Eupatoria*, the pappus of the *Compositæ*, &c., are described, and their development traced.

[2] Millington, American Naturalist, vol. ii. (1868). See also a discussion of this question by Warming in Tidsskrift f. popul. Fremstill. af Naturvidenskaben; 4 Række, Bd. i. p. 417; and Otto Norstedt's paper, Kunna bladen hos *Drosera*-arten äta Kott? (Botaniska Notiser, 1873, p. 97-102).

[3] American Naturalist, Dec. 1873; Nature, Feb. 26, 1874.

wards ; and when the plant is deposited in the collecting case the leaves are soon reflexed, and by their revolution conceal the root.

Irritability in the Stamens and Stigmas of Plants.—The stamens of the common berberry and various other plants are so excitable, that when the filament is brushed by an insect, or by any other point near the base, it will approach the pistil with a sudden jerk, so that the pollen is dislodged from the cells of the anthers (by means of a sort of "trap-door" on either side), and sprinkled on the stigmatic surface of the pistil. Jourdain[1] has found that the irritability of the stamens is suspended by chloroform, just as similar irritable movements in the leaves of other plants are.

In an Australian *Stylidium* the stamens and style form a united column, which is bent over to one side of the corolla; but if slightly irritated, it will immediately spring over to the opposite side of the flower. If the throat of *Schizanthus pinnatus* be slightly pressed, the stamens spring forward and discharge their pollen. In *Apocynum androsœmifolium* (dog's-bane) the anthers converge towards the nectaries, consisting of five glandular and somewhat oval bodies, which are sufficiently separated below to admit air to the anthers. As soon as a fly introduces its proboscis between the anthers from the top, they close so suddenly as to detain the fly a prisoner for life, for the insect generally perishes.[2] Similar irritability is displayed by the stigmas of *Martynia* and the style of *Goldfussia anisophylla*. Many other similar instances could be quoted,[3] but the above will suffice to illustrate this interesting subject. Why they should exhibit this irritability is unknown, no anatomical peculiarities which would account for it having as yet been observed.

Professor J. B. Schnetzler has attempted to explain it on other grounds than irritability. In some remarks on the stamens of the common berberry and other species of *Berberis*,[4] he was led to the belief that the term "irritability" or "contractility" of the vegetable tissue explains nothing of its real cause. Previous investigations by the same observer into the movements of the leaves of *Mimosa* and *Dionœa*, and of the stamens of *Parietaria*, had induced him to attribute some part of its production to the protean matter or protoplasm which constitutes a portion of the living cells

---

[1] Comptes rendus, April 25, 1870.

[2] The Physiology of Plants (Anonym.), Edin., 1835, p. 270.

[3] *E.g.*, in *Helianthemum vulgare* (where the motions of the pistils are even more remarkable than those of the stamens), *Parnassia palustris*, *Sparmania Africana*, *Cereus grandiflorus*, *Mimulus glutinosus*, *Bignonia* (stigma), *Maranta bicolor* (stigma), *Saxifraga tridactylites*, *Ruta graveolens*, various Cactaceæ, passion-flower, Cistus, nettle, pellitory, &c.

[4] Communicated to the "Société Vaudoise des Sciences Naturelles;" The Academy, 1869, p. 48.

(p. 20). The experiments which he made on the stamens of the berberry confirm in this respect those which he had previously made on the leaves of the sensitive plants. For instance, the ourali poison, which does not destroy the contractility of animal sarcode, and leaves untouched those same properties in protoplasm generally, has also no influence on the movements of *Mimosa*, nor on those of the berberry. On the other hand, nicotine, alcohol, and the mineral acids, destroy the life of sarcode and protoplasm, and the irritability of the leaves of Mimosa and of the stamens of berberry. This explanation is only one contribution to an explanation—not one in itself. The so-called irritability of the stamens of *Kalmia*, an American plant, is a mechanical act (p. 407, 440). The elastic, bursting pods of the Touch-me-not (*Impatiens noli-tangere*) come under the same category—*i. e.*, the movement is mechanical, not vital.

MOVEMENTS OF CLIMBING PLANTS.

Perhaps the most remarkable contribution to the history of "vegetable irritability," or, if you will, "instinct," which has been made of late years, are the remarkable observations of Charles Darwin on climbing plants.[1] As these observations open up a wonderfully fruitful field for inquiry, we will devote some space to a notice of a few of the more remarkable of them. A student ignorant of these researches is ignorant of some of the most important observations which have ever been made in his science. Climbing plants may be divided into (1.) those which spirally twine round a support; (2.) those which ascend by the movement of the petiole or tips of their leaves; (3.) those which ascend by true tendrils; (4.) those which are furnished with hooks; and (5.) those which are furnished with rootlets. The last two are not distinguished by any special movements, and the interest accordingly centres in the first three.

Spirally Twining Plants.—Both Darwin and Beal note cases in which vines will twine round a support, and after running above the support, still continue their spiral movements, "swinging around, following the course of the sun." In one case the movement lasted as long as the plant continued to grow, but each separate internode, as it grew older, ceased to move. In the case of the hop, and most other twining plants, about three internodes at a time partake of this motion. This particular vine performed a revolution in from one to two hours, moving most rapidly in the warmest part of the warmest day.

---

[1] On the Movements and Habits of Climbing Plants, 1866. See also Journ. Linn. Soc., 1865.

Hoya carnosa, one of the Asclepiadaceæ, revolves opposite to the sun in five or six hours, making a circle of over 5 feet in diameter. The tip traces 32 inches per hour. It is an interesting spectacle to watch the long shoot sweeping, night and day, this grand circle, in search of some object round which to twine. To prove that Mohl was wrong when he ascribed the revolutions to the twisting of the stem, it may be noted that *some* stems are not regularly twisted, and *others* twist in an opposite direction to the revolving plant. If a stick, shortly after having been wound around, be withdrawn, the climber will for a short time continue its spiral form, but soon it will straighten itself out, and again commence its revolutions in search of a fresh support. Experiments prove that stems do not in general twine, owing to a dull irritability of the stem, as Mohl imagined. If the support of a twiner be too short for it, it will fall to the ground, and then the tip will commence to climb afresh. Sometimes the flexible shoots of several climbers will form a cable, and thus support each other. Rarely do plants of the same order twine in opposite directions, and no two species of the same genus go in contrary directions, though most plants twine in a direction opposed to the sun. Climbers of temperate zones do not often climb round thick trees; while those of the tropics do, in order to reach light in the dense tropical jungle. In *Testudinaria elephantipes*, according to Mohl, it is only the branches, not the stem, which revolve; and in the asparagus, on the other hand, it is the leading shoot, not the branches, which revolves and twines. The twining of some is regulated by the season—twining, as they do, in the summer, and not in the autumn; and the climate also alters their habits in this respect, plants which grow erect within their native country twining in this. They will also show an *antipathy*, if the term may be used, to certain trees, and refuse to climb around these if even they be close at hand. For instance, M. Paul Lévy noticed that the lianas of Central America will not attach themselves to particular trees, even when brought into juxtaposition with them; and these trees thus slighted are just those which are most unsuited for the purposes of twining plants—viz., smooth-stemmed, umbrella-topped species. This antipathy of the climbing plants to these trees is also, to a less extent, shown by moss, ferns, orchids, Bromeliaceæ, and other epiphytal plants.[1]

Leaf-Climbers.—The stems of several species of *Clematis*, *Lophospermum*, *Maurandia* (all flowering garden-plants), are twiners like the hop, &c. "But in addition to this mode of holding fast, the petioles are sensitive to the touch, slowly bend in the form of hooks, and if successful in catching a stick, they clasp it firmly, and soon become greatly enlarged and strengthened by an extra

---

[1] Cited by Masters in Gardeners' Chronicle, 1870, p. 383.

growth of woody fibre. If they come in contact with no object, they retain this position for a considerable time, and then, bending upwards, they reassume their original upturned position, which is retained ever afterwards." Some petioles are so sensitive that they will catch firmly at anything they feel the weight of—withered blades of grass, soft young leaves of a maple, or flowering peduncles of the quaking-grass (*Briza*). In *Tropæolum tricolorum*, var. *grandiflorum*, a remarkable fact has been noticed—viz., that the petioles of young leaves, if they catch no object after standing in their position for some days, will move gradually towards the stem, oscillating a little from side to side as if in search of the needful support. The flower-peduncles of *Maurandia semperflorens* (order *Scrophulariaceæ*) are sensitive like tendrils, and exhibit revolving powers which seem of no service to the plant, as it loses the power when the flower is old enough to open. In *Solanum jasminoides*, as in no other leaf-climber yet noticed, a full-grown leaf is capable of clasping a stick; but the movement is extremely slow, requiring several weeks. The effect of this is to much increase the thickness of the petiole. Plants belonging to eight orders are known to have clasping petioles, and plants to four families climb by the tips of their leaves. With rare exceptions, the petioles are sensitive only when young; they are sensitive on all sides, but in different degrees in different plants. If rubbed with a piece of wood, these leaf-climbers will generally respond to the irritation by curving in the course of two or three days. This shows that climbing in these plants is the result of a movement under sensitiveness of touch, no matter how slow that may be.

Tendril-Bearing Plants.—Plants belonging to ten orders are tendril-bearers. Between leaf and tendril climbing there are all gradations. For instance, look at the tendril of the pea, which is only the developed end of the midrib. In *Nepenthes*, the prolongation of the leaf, at the end of which the pitcher is placed, twines; in *Gloriosa*, the end of the leaf is developed into a hook; while in *Cobæa*, the grapples and hooks by which it climbs so vigorously are only the upper portions of a compound leaf changed into tendrils—and the same is true of the tendrils of the pea, &c. Species of *Bignonia* and a few others afford connecting-links between climbers, leaf-climbers, tendril-bearers, and root-climbers. "Some little time after the stem of *Bignonia Tweedyana* has twined round an upright stick, and is securely fastened to it by the clasping petioles and tendrils, it emits at the base of its leaves aerial roots, which curve partly round and adhere to the stick; so that this one species of *Bignonia* combines four different methods of climbing generally characteristic of distinct plants—namely, twining, leaf-climbing, tendril-climbing, and root-climbing." The movements of *Bignonia venusta* are very complicated. Not only the tendrils, but the petioles bearing them, revolve—these last, however, being in no way sensitive; and all the parts revolve at a different rate, and quite independent of each other. In a few days after the tendrils have clasped the stem, their extremities often become developed into irregular disc-like balls, which have the singular power of adhering firmly to the wood. The undivided tendril of *Bignonia speciosa* ends in an almost straight, sharp, uncoloured point, and the whole exhibits a trait which, if seen in an animal, would be called instinct, for it continually searches in its movements over the surface of the wood for any little dark hole in which it may insert itself. Mr Darwin tells us that the same tendril would frequently withdraw from one hole and insert its point into a second one. "Improbable as this view may be," Mr Darwin remarks, "I am led to suspect that this habit in the tendril of inserting its tip into dark holes and crevices may have been inherited by the plant after having lost the power of forming adhesive discs."

The tendrils of a plant of *Bignonia capreolata* sought the darkness and avoided the light unerringly. When a tendril does not succeed in clasping something, it bends downward to its own stem, which it seizes; and if it seizes nothing, it soon withers and drops off. In *Corydalis claviculata* we have an instance of a regular transition from a leaf-climber to a tendril-bearer, its tendrils still bearing leaflets, though very much reduced in size. In *Echinocystis lobata*, and other plants, the tendril will—though only touching a support placed some distance from the plant—in a few hours curl twice or thrice around the stick by a sort of vermicular motion—"just as a strong man, suspended by the ends of his fingers to a horizontal pole, works his fingers onwards until he can grasp the pole with the palm of his hand." Though the tendrils of plants belonging to *Vitaceæ*, *Sapindaceæ*, *Passifloraceæ*, &c., may be modified peduncles, their homological nature makes no difference in their actions. In *Ampelopsis*, or Virginia creeper, discs are developed at the end of the tendrils (p. 125).

"In revolving tendrils, the most wonderful thing is the way in which they avoid winding themselves round the stem they belong to. The active tendrils are, of course, near the top of the stem or branch. The growing summit beyond the tendril, now seeking a support, is often turned over to one side, so that the tendril, revolving horizontally, has a clear sweep above it; but as the stem lengthens and rises, the tendril might strike against it, and be wound up and around it. It never does. If we watch these slender passion-flowers, which show the revolving so well on a sultry day, we may see with wonder that when a tendril, sweeping horizontally, comes round so that its base nears the parent stem rising above it, it stops short, *rises stiffly upright, moves on in this position until it passes by the stem, then rapidly comes down again to the horizontal position*, and moves on so until it again approaches and avoids the impending obstacle."[1]

Spiral Contractions.—It is seen that the tendrils of several kinds of plants, if they catch nothing, contract, after an interval varying from a day or two to several weeks, into a close spire, and "a few into a helix." The tendrils are thus made highly elastic, so that a plant with this coiled tendril can "safely ride out the gale, like a ship with two anchors down, and with a long range of cable ahead to serve as a spring as she surges to the storm." A tendril which is uncaught contracts spirally always in the same direction from tip to base; while, if the contrary is the case, it invariably becomes twisted in one part in one direction, and in another part in another direction, the oppositely twined spires being separated by short straight portions. Many extremely interesting observations of a like nature have been made. Some tendrils are excessively sensitive, the slightest touch causing them to become hooked. After a touch, the tendril of *Passiflora gracilis* moved in twenty-five seconds. Many of the tendril-bearing plants come from the American continent, and possibly a connection might be traced between this and the abundance of arboreal animals (?).

Root-Climbers.—These we have referred to when describing the root. The rootlets of *Ficus repens* emit minute drops of clear fluid, slightly viscid, to assist its upward progress—and so on.

Now, what does all this tend to? No doubt plants become climbers in order to reach the air and light, and in climbers this is effected with very little expenditure of organised substance, compared with trees which have huge solid trunks to enable them to do the same.

Darwin thinks, in accordance with the well-known views which are associated with his name, that because these climbing plants graduate into one another, they have become climbers by gradual change, and that leaf-climbers were primordially twiners, and tendril-bearers were primordially leaf-climbers. He believes that the capacity of acquiring the revolving power, on which most climbers depend, is inherent, though undeveloped, in almost every plant in the vegetable kingdom.[2] Whether this is so or not the student must determine for himself. Theory apart, the facts are strange enough to excite wonder and inquiry. They look almost instinctive; yet in the present state of our knowledge we must, almost with a yearning after something more, call them merely displays of "vegetable irritability."

---

[1] Gray, How Plants Behave, p. 18 (1872).

[2] See Beale in American Naturalist, p. 405-419.

What, then, is this Vegetable Irritability? — We have already alluded (p. 578) to Schnetzler's attempted explanation, but what does it amount to? We may explain how the motions are accomplished; but when we come to consider how one mass of tissue in one particular plant has this power, and the same tissue, differing in no appreciable degree in appearance, in another part of the same or a different species or individual, wants it, we arrive at a problem which it is beyond our present knowledge to solve. The probability is, that most of these movements consist either in shortening the cells on the concave side, or elongating them on the convex side. Gray has pointed out—what is perfectly to the point—that stems curved towards the light, curve still more when the convex side is cut away, thus showing that the cause of the curvature is due to the contraction of the cells on the concave side. In *Impatiens* (p. 579) the phenomenon of the elastically bursting body confirms this view. Here the valves of the capsule curve inwards very strongly when liberated in dehiscence: and that this is owing to the shortening of the cells of the inner layer, and not to the enlargement or turgescence of those of the thick outer layer, is readily shown by gently paring away the whole outer portion before dehiscence; for the inner layer, when liberated, still incurves and rolls itself up as strongly as before. The short valves at the summit of the pod of *Echinocystis* slowly curve outward in dehiscence: here the cells of the outer layer of the valve are longer and narrower than those of the inner, and the latter are stretched and torn in opening; so that here the contraction of the cells on the side which becomes concave is undoubtedly the cause of the movement. And since muscular movements are effected by the contraction of the cells, which, placed end to end, compose a muscular fibril, we may suspect that vital movements generally, both in vegetables and animals, are so far analogous that they are brought about in the same general way—viz., by the shortening of the cells. We have seen that the opening and closing of the stomata is effected by a change in the form of the cells forming them; and probably this is effected by the vital force. However, how light or other causes affect the cells to secure this shortening or elongation, we know not.

The student ought, however, to bear in mind, that in plants we have never yet discovered anything either analogous to, or homologous with, the nervous system as found in the higher animals, though various botanists have not hesitated to look upon these movements as due to something of the kind. There is, however, no denying that as we approach the confines of the animal and vegetable kingdoms, the developments of life are exceedingly similar; so much so, indeed, that Ernst Haeckel has proposed—

perhaps on insufficient grounds—to group these organisms, which combine the characters of both kingdoms, into a separate one—his *Regnum protisticum.* In the protozoa there is no trace of a nervous system, yet it is a familiar fact to every zoologist that they contract and perform vital movements with the greatest readiness; and even in some higher animals, where no nervous system has as yet been detected, very complex vital movements are performed—apparently quite as much due to "animal irritability" as those described in the preceding paragraphs are to "vegetable irritability." Finally, in the words of Asa Gray, whose pertinent remarks on this subject it would be unjust not to quote in full: "When we consider that the excitability of sensitive plants is often transmitted, as if by a sort of sympathy, from one part to another; that it is soon exhausted by repeated excitation, . . . to be renewed only after a period of repose; that all plants require a season of repose; that they consume their products and evolve heat under special circumstances, and with the same results as in the animal kingdom; that, as if by a kind of instinct, the various organs of the vegetable assume the position or the directions most favourable to the proper exercise of their functions and the supply of their wants, to this end surmounting intervening obstacles; when we consider in this connection the still more striking cases of spontaneous motion that the lower Algæ exhibit, and that all these motions are arrested by narcotics, or other poisons—the narcotic and acrid poisons even producing effects upon vegetables respectively analogous to their different effects upon the animal economy,—we cannot avoid attributing to plants a vitality and a power of 'making movements tending to a determinate end,' not differing in nature, perhaps, from those of the lower animals. Probably life is essentially the same in the two kingdoms, and to vegetable life faculties are superadded in the lower animals, some of which are here and there not indistinctly foreshadowed in plants."[1]

---

[1] Op. cit., p. 350.

CHAPTER IV.

ODOURS, COLOURS, LUMINOSITY, TEMPERATURE, AND NOSOLOGY OF PLANTS.

THE various delightful or disagreeable odours of plants generally reside in the flowers, though in some the leaves or other portions are the seat of these ; but in both cases the odour is due to the presence of essential oils, or other glandular product, in the epidermis of the odoriferous organ.

Some flowers only smell powerfully at night, and not during the day. These Linnæus called *flores tristes*, or melancholy flowers. They belong to various orders and tribes, as discordant as possible, but agreeing in the peculiarity named, and in the fact that in all of them the odour is very delicious, and in the fact that they all bear pale-yellowish or brownish-tinted flowers. Examples of such plants are *Mesembryanthemum noctiflorum*, *Pelargonium triste*, *Hesperis tristis*, *Cheiranthus tristis*, *Crassula odoratissima*, &c. Some others, which exhale a most powerful lemon-like scent, are great favourites with the Chinese, but bear no resemblance to each other, or have anything in common except in the hue of their blossoms. Again, various plants belonging to very different orders have a camphorous odour. The sweet smell of hay is found not only in the grass called *Anthoxanthemum odoratum*, but in woodruff (*Asperula odorata*), melilot (*Melilota officinalis*), and all the varieties of *Orchis militaris*—plants all differing widely from each other in botanical characters. Their odour, moreover, has one peculiarity, in that it only begins to be perceptible when the plants yielding it begin to dry. It proceeds from their whole herbage, and would seem to escape from the orifices of its containing cells, only when the surrounding vessels, by growing less turgid, withdraw their presence from such orifices. When the scent of new hay is vehement, it becomes then like the flavour of bitter almond, and in some people gives rise to "hay fever." Perhaps it may be cited as analogous to this identical odour being yielded from otherwise dissimilar plants, that the taste of capillaire syrup, given by an infusion of orange-flowers, is found in the foliage of *Gaultheria procumbens* and in meadow-sweet (*Spirea ulmaria*)—two very dissimilar plants, belonging respectively to the orders of Ericaceæ and Rosaceæ.[1] We are told by Mr Bateman that in the order *Orchidaceæ* alone may be found the odours of honey, musk, citron, allspice, cinnamon, noyau, angelica, aniseed, pomatum, violets, wallflowers, fresh hay, and cocoa-nut milk; and similar instances from other orders might be cited.

Some plants have a very disagreeable instead of a pleasant smell. For instance, *Pæderia fœtida*, an African plant, excites fever and headache in those inhaling its odour; a smell as of decayed animal matter is given off by the carrion-plant (*Stapelia*); while the odour of the "skunk-cabbages" (*Symlocarpus, Pothos*) of America, is sufficiently expressed by their popular name.

Some plants only give out their odour during the opening of the flower; others only give it out at night; while in another class it is only yielded at particular periods.

In *Epidendrium cuspidatum*, Lindl., an exotic orchid, M. Rivière found a curious periodicity. It exhaled a pleasant odour at five o'clock in the morning, and remained inodorous until the following night. On the other hand, *E. cochleatum*, Lindl., var. *fragrans*, gives forth a fragrance like that of the hyacinth between 6 A.M. and 6 P.M.; the perfume of *Cattleya bulbosa*, Lindl., is only exhaled between 6 A.M. and 9 A.M.; while that of *Angræcum distichum*, Lindl., is exhaled between 11 A.M. and 6 P.M. Finally, to finish the enumeration of the peculiarities of the odour of these orchids, it may be mentioned, on the authority of M. Duchartre, that the flower of *Rodriguezia crispa* commences to give out its scent at 6 A.M., and continues to do so to 11 P.M. In most cases, flowers lose their odour during the heat of mid-day; while the night-flower, *Cereus grandiflorus*, emits its powerful fragrance at intervals of a quarter of an hour during the brief period of the expansion of the flower.

In reference to odours given forth at particular times, M. Rivière observed that in an araceous plant of the genus *Conophallus*, from Cochin China, the female flowers exhaled an odour just at the moment when the male flowers, situated a little higher up on the same common axis, opened their stamens to shed the pollen, after which the odour disappeared. A similar observation was made by Warming regarding the *Philodendron* he examined (p. 598), and Morren found that a *Maxillaria* ceased to give forth its aromatic odour after the pollen was applied to the stigma.

There seems to be some analogy between the smell and the colour of flowers. For instance, *Chrysanthemum Indicum*, with orange-coloured flowers, agrees faintly in scent, as it does in

---

[1] See Sir J. E. Smith's Introduction, &c., p. 44 (ed. 1836), and Grew's Anat. of Plants, p. 279-292, for a further expansion of the facts which we have noted.

colour, with the common wallflower (*Cheiranthus Cheiri*). It has been found that white flowers have the greatest average of pleasant-smelling ones; orange and brown flowers are often disagreeably scented; while the order which has the most odoriferous flowers is not, as commonly supposed, the *Rosaceæ*, but the *Nymphæaceæ*, to which the water-lilies belong. An analogy might also be traced between taste and smell, in so far that the two are strongly connected, and with many people almost undisseverable—so much so, that unless the flower is smelt there is no taste perceived; nor can the difference of taste be appreciated without the eye and nose being called in to assist the gustatory nerve.

The roots of some plants (*e.g.*, *Arum maculatum*) have, when fresh, a most acrid taste and irritant quality, though, when dry, they become farinaceous and inert.

The *use* of taste and odour is not very apparent. Plants might have been less odoriferous or sapid without at all disarranging their functions; but no doubt these qualities are not there except to serve some wise purpose, or to serve to the gratification of man's senses. Possibly they may be connected with the fertilisation of plants by means of insects.

Classification of Odours.—Various attempts have been made from time to time—among others, by Linnæus—to classify odours. The latest of these attempts is by M. Fée.[1] The following is a synopsis of this classification:—

1. *Odorous bodies:* (α) Superodorants; (β) Subodorants. 2. *Nidorous bodies:* (α) Supernidorants; (β) Subnidorants.

A. *Odorous bodies:* (α) Superodorants are substances which have an agreeable perfume, which is often owing to volatile oils, which are distilled for the sake of their scent. He divides these odours into *camphorous* (odour of camphor), *citronous* (odour of citron and orange), *myrtilloid* (odour of myrtle), *anisoid* (odour of aniseed), *rhodoid* (odour of the "hundred-leaved rose"), and *anthemisoid* (odour of camomile). When the odours are owing to the presence of resins, they are divided as follows: *Balsamoid* (balms, vanilla). Certain odours of an analogous nature are owing to principles not yet determined. These are as follows: *Nardosmoid* (Tussilago, Nardosmia fragrans), *Ambrosoid* (Chenopodium ambrosioides), *Moschoid* (Erodium moschatum, Scandix odorata, &c.), *Narcissoid* (Narcissus poeticus, N. Jonquilla, Lilium candidum, Polianthes tuberosa, &c.), *Violet* (Viola odorata, wallflower, Matthiola, mignonette, &c.)

Subodorants are those in which there is a mild, agreeable odour. The following are the classes: *Meliosmoid*[2] (Galium verum,

---

[1] Mém. de la Soc. Roy. Bot. Belge, cited in St Pierre, l. c., p. 960.

[2] Honey odour.

flowers of lime), *Jasminoid* (odour of jasmine), *Amygdaloid* (odour of bitter almonds, Sambucus herbacea, &c.), *Cyamoid* (flower of acacia, Robinia Pseudacacia, Lathyrus odorata, &c.), *Maloid* (odour of apple), and *Tannoid* (odour of tanned leather).

B. *Nidorous bodies* are those in which the odour is strong, and often disagreeable, and are divided into super and sub-nidorants, according to the intensity of the odour. Fée divides them into the following classes: 1. Odours due to volatile oils holding resin in solution, and isolable by distillation — *Terebinthoid* (Coniferæ, Terebinthaceæ, &c.) 2. Odours due to volatile oils—*Peganoid* (odour of rue, *Ruta graveolens*), *Dictamnus*, *Tagetes patula*. 3. Odours due to the presence of sulphurous oil—*Allioid* (odour of garlic), asafœtida, acacia-roots, &c. 4. Odours due to different principles—*Fetid* (various species of Sterculia, Datura, Nicotiana, and other Solanaceæ), *Mecanoid* (odour of opium and poppies), *Cicutoid* (Conium maculatum, &c.), *Hircoid* (odour of the goat, Hypericum hircinum, Loroglossum hircinum), *Ciminoid* (Coriandrum sativum, Coris Monspeliensis), *Pteridosmoid* (fern odours); and lastly, there are the following odours: *cadaverous*, *marine*, *spermatic*, *sterculine*, *urinous*, and *vulvary*.

The different kinds of odours have brought certain descriptive terms into use to designate them. These are (in Latin) *alliaceus*, *ambrosiacus*, *aromaticus*, *fœtidus* (or *teter*), *graveolens*, *hircinus*, *muriaticus*, *pungens*, *spermaticus*, *suaveolens*, *virosus*, &c., most of which are explained above, or are self-descriptive.

COLOURS OF PLANTS.

With the exception of the parts composing the flower, the epidermis is in general coloured green, owing to the presence of chlorophyll. Occasionally, however, it is variegated, especially in the leaf, which is frequently differently coloured on the under and upper surfaces. For instance, the leaves of *Begonia* are satiny-green above, and traversed by dark-red veins on a reddish ground beneath. When plants naturally green become variegated, it is primarily a diseased state; but this state can be, and is, frequently transmitted to the posterity of the plant by the art of the horticulturist. Variegated plants have generally less vital energy than uniformly coloured ones. Plants of an acid or astringent nature often become very red in their foliage by the action of an acid, as the dock, *Epilobium* and *Berberis*. A most extraordinary change of colour has, however, been observed in a *Selaginella* (*S. mutabilis*) cultivated in the Royal Gardens at Kew. In the morning the fronds are green, but as the day advances they become pale, recovering gradually their colour by the following day. Dr

Hooker observed that in their pale condition the endochrome, or colouring matter of the cells, was contracted into a little pellet.[1] Changeable colours are also found in the corollas of flowering plants. For instance, that of *Hibiscus mutabilis* is white in the morning, pale-rose at mid-day, and bright-rose in the evening. Some white flowers (*e. g.*, the white flowers of the margin of *Chrysanthemum alpinum*) redden as they fade. In these *flowers*, however, we have the most varied and exquisite colours—adding immensely to the beauty of the plants. These colours also undergo remarkable variations. For instance, in the little English scorpion-weed (*Myosotis scorpioides*), and several others of its natural order (*Boraginaceæ*), the flower-buds are of the most delicate rose-colour, which turns to bright blue as they open; and many yellow flowers, under the influence of light, become white. Numbers of red, blue, or purple ones are liable, from some unknown cause, to vary to white. Such varieties are sometimes propagated by seed, but can in general be kept up if the plant is propagated by cuttings, grafting, or by roots.

Classification of Colours.—The researches of De Candolle primarily, and in the second degree of Schübler and Frank, have established the following classification of the colours of plants. They are divided into two series—*Cyanic*[2] (of which blue is the type), and *Xanthic*[3] (of which yellow is the type). From these proceed all the various tints, according to the following chromatic scale:—

Red. Orange-red. Orange. Orange-yellow. Yellow. Yellow-green.	Xanthic series of De Candolle (oxidised series of Schübler and Frank).
Green.	Colour of leaves.
Blue-green. Blue. Blue-violet. Violet-red. Red.	Cyanic series, DC. (desoxidised series of Schübler and Frank.)

When we examine the plant microscopically, we find that in general the colours of the cyanic series are in solution in the juice of the cells, while those producing the xanthic series and the green are in the form of granules, which are only modifications of chlorophyll. Exceptions to this rule, however, exist—according to Mohl and George Lawson—in the flowers of *Strelitzia Reginæ* and *Salvia splendens*, in both of which the colouring matter exists in a granular form.

---

[1] Berkley, Introd. to Cryptogamic Bot., p. 562.

[2] κυανός, blue.

[3] ξανθός, yellow

The different shades of the same colour in flowers are produced by the greater or less number of colourless cells interspersed through the substance of the coloured ones, and the different colours are often caused by layers of cells with one colour lying above another with a different colour (*e.g.*, brown by red above green, orange by yellow above red, &c.) White is generally produced by cells containing air, and this is also the cause of the white spots on some green or other coloured plants.

The velvety appearance of many flowers and leaves is caused by the play of the rays of light on the epidermis, the superficial cells of which are raised into papillæ (fig. 33, p. 53); and the metallic tint of the leaves of certain orchids is due to the action of light on prismatic cells containing air.

The Relation of Form and Colour.—It would be neither just to the student, nor to the distinguished botanist, to whose labours we are indebted for them, to pass from this subject without noticing, however briefly, the beautiful researches of Professor Dickie of Aberdeen on the relations of form and colour.[1] By means of patient research, conducted over a number of years, he has deduced some remarkable laws, which may be given *seriatim.*

1. *In regular corollas the colour is uniformly distributed, whatever be the number of colours present*—that is to say, the pieces of the corolla, being all alike in size and form, have each an equal proportion of colour. The common primrose (*Primula vulgaris*) is an example where the petals are all of one colour. In the Chinese primrose (*Primula sinensis*) there are two colours. Here the centre is yellow and the margin purple, but each has an equal proportion of colour.

2. *In irregular flowers where the number* 5 *prevails, the odd piece is most varied in form, size, and colour; when only one colour is present, it is usually more intense in the odd lobe of the corolla.* Where there are two colours, one of them is generally confined to the odd piece. Sometimes, when only one colour is present, and of a uniform intensity in all the pieces, the odd segment has spots or streaks of white. For instance, in the common laburnum there are four petals yellow, and the fifth yellow with purple veins. In the common red clover the odd piece is distinguished from the others by its darker purple veins.

In the eyebright (*Euphrasia officinalis*) the corolla is generally purple; the odd piece has a yellow spot. In the *wild thyme* the corolla is generally red-purple, with two pale spots on the odd piece. And in *Ajuga reptans* (common bugle), four divisions are purple, and the fifth has a yellow spot on the inner surface.

It has also been pointed out, by various observers, that when a

---

[1] Typical Forms and Special Ends in Creation, by Principal M'Cosh and Professor Dickie, 1857, p. 153.

flower is of two colours, the one is always a complement of the other—*e. g.*, *Primula farinosa*, bearing pale-lilac blossoms, "with yellow eyes powdered with silver farina." When there are three colours, the third is commonly white.[1]

3. *In certain Thalamiflorous Exogens* (*i. e.*, flowers where there is no adhesion between the whorls of the corolla, and where the stamens are hypogynous or inserted at the base of the ovary) *with unequal corolla, arising chiefly from difference in size of the petals, the largest are most highly coloured*—*e. g.*, the common horse-chestnut. On each petal there is usually a crimson spot at the lower part; the size of this spot and its intensity are in direct relation to the size of each petal—the two upper being largest, and the two lateral smaller, and the odd piece least of all.

4. *Different forms of corolla in the same inflorescence often present differences of colour, but all of the same form agree also in colour.*

The Compositæ (Aster, daisy, &c.) illustrate this. Where there are two colours, the flowers of the centre, usually of tubular form, have generally one colour of uniform intensity. Those of the circumference having a different form, agree in colour also—*e. g.*, daisy, where the centre flowers are yellow, and all the ligulate or strap-like flowers of the ring or circumference are white, variegated with purple. A yellow centre with a purple margin is common in Compositæ—*e. g.*, *Aster*, *Rudbeckia*, &c.

5. *The law of contrasts in the colours of the flowers is simpler in Monocotyledons than in Dicotyledons.*

The flowers of Dicotyledons may be symbolised by the square or pentagon—four, eight, five, or ten being the prevalent numbers in the different whorls; whereas, since three and six are generally found in the flowers of Monocotyledons, the triangle may serve to symbolise such an arrangement.

In conclusion, it may be stated that *simplicity of figure corresponds with simpler contrast of colour in the Monocotyledons; while greater complexity of colour, and greater complexity of structure, are in direct relation to Dicotyledons.*

Is all this mere coincidence? Professor Dickie (than whom no man's opinion is entitled to more deference) thinks that it is not. The laws of beauty not being yet unfolded and detected, this author remarks that it is not possible to demonstrate scientifically that the relations we have been treating of are in accordance with artistic principles. "Still the eye at once perceives, in regard to some of these arrangements, they are intended to enhance the beauty of the plant. Would not reason be offended if uniform flowers had not uniform colouring? And is there not propriety when, in an irregular flower, there is one petal standing by itself,

---

[1] Gillman in Amer. Naturalist, 1870, p. 313.

that that petal should have more brilliant colours, that thus the flower may be tempered together, having more abundant honour in the parts which lacked, that there be no schism in the plant?" In all this there is an adaptation of the colour to the natural taste of man, and to the laws of colouring to which that taste has given rise. For instance, in painting, a large portion of the ground is of a neutral colour; and in the grand canvas of nature, the ground-colours, if not neutral, are soft and retiring. The sky is not scarlet, nor the clouds crimson, nor the grass yellow, nor the trees decked with orange-leaves. The soil, on the contrary, is in most places a sort of brown; the mature trunks of trees take a neutral tint; the sky is soft blue, except where covered with grey clouds; and the foliage of the earth is refreshing green. There is also a beauty in the way different plants grow together in association; in a word, in nature we see the most exquisite harmony of colours in association — laws which have been only recognised by man in a late state of his civilisation, though ever existing in the vegetable world. If Mr Darwin's theory is true, then there can be nothing in this; for he allows only utilitarianism, or descent, as at all concerned in the varieties of colour, &c., though to the artistic mind this is one of the objections to the doctrines of the eminent philosopher mentioned. In science, however, we can afford the indulgence of no æsthetic sentimentalism, and the doctrine must stand or fall by facts. In the mean time, it will be enough that we state the facts, as generalised by this most eminent of Scottish botanists.

LUMINOSITY OF PLANTS.

It has been long known that certain plants emitted light, which, for want of a better name, has been called phosphorescence. The numbers known to do so are rather numerous, and belong to different orders. Not to mention the vague rumours of fiery bushes which still float about in India among the modern Hindoos, as such stories did in former days among the old Hindoos and Greeks, there are facts, circumstantial and well confirmed, enough to record.

Luminosity of Roots, &c.—The root-stock of a plant from the Ooraghum jungles, at the foot of the Madura Hills, near Tachoor in India, was exhibited in July 1845 at a meeting of the Royal Asiatic Society. It lost its phosphorescence when dry, but regained it when moistened; and this property was not lost by repeated experiment each time it was tried—the slice of the root glowed with equal brilliancy. It is said that this plant has been long familiar to the Brahmins under the name of Jyotismati, and that the discovery of its phosphorescence was made by a "tuhseeldar" compelled to take shelter at night under a scrap of rock, when he was astonished to see a blaze of phosphoric light all over the grass in the vicinity. The Sanscrit authorities also refer to it.

The late Colonel Madden found that perhaps one root in a hundred of *Anthistiria Anatherum* was luminous at night during the rainy season in the Himalayas, where it is found. Other grasses, such as species of *Andropogon*, are reported to possess the same property; and fakirs seek far and near for a plant they call "Sunee," which is rumoured to possess this quality also, in addition to the more mythical one of revealing the wonders of fairyland.

Luminosity of Flowers.—In 1845, the country around Simla in the Himalayas was filled with rumours that the mountains near Syree were illuminated nightly by some magical herb. Probably these rumours may be traced to the existence of luminosity in *Dictamnus Himalayensis* (Royle), or other species of the same genus, which is known to possess that property in its European representative *D. albus*. *Polianthes tuberosa* is rumoured, though doubtfully, to dart small sparks in great abundance, in a sultry evening after a thunderstorm, from such of its flowers as are fading. In regard to the phosphorescence of the Dittany, or *Fraxinella*, much doubt has been expressed; but of late the matter has been experimentally set at rest by the observations of Dr Hahn,[1] who remarks: "When the daughter of Linnæus one evening approached the flowers of *Dictamnus albus* with a light, a little flame was kindled without in any way injuring them. The experiment was afterwards frequently repeated, but it never succeeded; and whilst some scientific men regarded the whole as a faulty observation or simply a delusion, others endeavoured to explain it by various hypotheses. One of them especially, which tried to account for the phenomenon by assuming that the plant developed hydrogen, found much favour. At present, when this hypothesis has become untenable, the inflammability of the plant is mentioned more as a curiosity, and accounted for by the presence of etheric oil in the flowers. Being in the habit of visiting a garden in which strong healthy plants of *Dictamnus albus* were cultivated, I often repeated the experiment, but always without success, and I already began to doubt the correctness of the observation made by the daughter of Linnæus, when, during the dry and hot summer of 1857, I repeated the experiment once more, fancying that the warm weather might possibly have exercised a more than ordinary effect upon the plant. I held a lighted match close to an open flower, but again without result; in bringing, however, the match close to

---

[1] Seemann's Journal of Botany, 1863.

some other blossoms, it approached a nearly faded one, and suddenly was seen a reddish, crackling, strongly shooting flame, which left a powerful aromatic smell, and did not injure the peduncle.[1] Since then I have repeated the experiment during several seasons; and even during wet, cold summers, it has always succeeded—thus clearly proving that it is not influenced by the state of the weather. In doing so I observed the following results, which fully explain the phenomenon: On the pedicels and peduncles are a number of minute reddish-brown glands, secreting etheric oil. These glands are but little developed when the flowers open, and they are fully grown shortly after the blossoms begin to fade, shrivelling up when the fruit begins to form. For this reason the experiment can succeed only at that limited period when the flowers are fading. Best adapted for the purpose are those panicles which have done flowering at the base, and still have a few blossoms at the top. The same panicle cannot be lighted twice. The rachis is uninjured by the experiment, being too green to take fire, and because the flame runs along almost as quick as lightning, becoming extinguished at the top, and diffusing a powerful incense-like smell." Various plants probably give forth inflammable matter, and it is probably for this reason that the natives of the Spice Islands are careful how they bring flame near particular trees.

Mr R. Dowling,[2] again, mentions the luminous appearance of the common marigold after a week of very dry weather in August. It occurred about 8 P.M., when a golden-coloured lambent light appeared to play from petal to petal of the flower, so as to make a more or less interrupted corona round its disc. It was less lurid as the light declined. Linnæus, his daughter Christina Linnæus, Linnæus the younger, Haggren, Crome, Zawadski, Hagen, Johnson, and the Duke of Buckingham, have contributed observations on this subject. The following plants have, in addition to those mentioned, been noted as luminous: Indian cress (*Tropæolum majus*), the sunflower (*Helianthus annuus*), the marigold (*Calendula officinalis*), African and French marigolds (*Tagetes erecta* and *T. patula*), Martagon lily (*Lilium chalcedonicum* and *L. bulbiferum*), poppy (*Papaver orientale*), hairy red poppy (*Papaver pilosum*), Chrysanthemum (*Chrysanthemum inodorum*), evening primrose (*Œnothera macrocarpa*), *Gorteria rigens*, geraniums, and verbenas.[3]

Regarding the last-named plant, a correspondent of a horticultural journal[4] noted the luminosity very particularly in reference

---

[1] The late Professor Henslow made a similar observation.

[2] Report of Brit. Assoc., 1843.

[3] Edwin Lankester in Gardeners' Chronicle, 1843, p. 691.

[4] Gardeners' Chronicle, 1859, p. 604.

to three scarlet verbenas, each about nine inches high and about a foot apart, planted in the border in front of his greenhouse.

"As I was standing a few yards from them, and looking at them, my attention was arrested by faint flashes of light passing backwards and forwards from one plant to the other. I immediately called the gardener and several members of my family, who all witnessed the extraordinary sight, which lasted for about a quarter of an hour, gradually becoming fainter, till at last it ceased altogether. There was a smoky appearance after each flash, which we all particularly remarked. The ground under the plants was very dry; the air was sultry, and seemed charged with electricity. The flashes had the exact appearance of summer lightning in miniature. This was the first time I had seen anything of the kind, and having never heard of such appearances, I could hardly believe my eyes. Afterwards, however, when the day had been hot, and the ground was dry, the same phenomenon was constantly observed at about sunset, and equally on the scarlet geraniums and verbenas. In 1859 it was again seen. On Sunday evening, July 10 of that year, my children came running in to say that the 'lightning' was again playing on the flowers. We all saw it, and again on July 11. I thought that the flashes of light were brighter than I had ever seen them before. The weather was very sultry."

The writer of these pages has also observed it frequently in *Tropæolum*, verbenas, and other plants, but cannot coincide with the theory of Allman and others that there is no real light, only an optical delusion. Whatever may be the cause, we have to seek it elsewhere than in this Gordian solution of the question.

There seems, however, more reason to believe that in mosses it may be due to simple reflection of light. *Schistostega pinnata*, a moss inhabiting caverns and dark places in the south of England, has been observed to give forth an appearance of light; but Babbington and Lloyd discovered that this luminous appearance was due to the presence of small crystals in its structure, which reflected the smallest portion of the rays of light. In Germany it has been observed in another species of the same genus—*S. osmundacea*—by Funk, Brandenberg, Nees von Esenbeck, Hornschuh, and Struve. By Bridel, Brideri, and Agardh the elder, it was attributed to the presence of a small Alga, *Protococcus smaragdinus*, which inhabited the moss; but Unger and Meyen have satisfactorily proved that "at certain seasons the cells of the moss assume a globular form, and being partially transparent, the light is refracted and reflected in such a way as to present a luminosity on the surface of the vessels."

Luminosity of Fungi.—Certain fungi have long been known to be luminous, this luminosity having been observed in various parts of the world; and it has been generally found to be a species of *Agaricus* which has yielded the phenomenon—*e.g.*, *Agaricus olearius* of the south of Europe, *Agaricus Gardneri* in Brazil, and by others in Australia, Amboyna, &c. The *Rhizomorphæ*, found in mines, are often so beautifully phosphorescent that one can see to read by the light given forth. A remarkable instance is recorded by the Rev. M. J. Berkley. A log of spruce of larch, 24 feet long, had the inside of its bark covered with a white byssoid mycelium. This was so luminous, that when wrapped in five folds of paper the light penetrated through all the folds on either side as brightly as if the specimen was exposed.[1] Diseased potatoes, on being sliced, are sometimes seen to be luminous, probably from the presence of a fungus causing the disease. A fungus, described by Drummond[2] as growing in the vicinity of the Swan River, gives out light enough to read by—the light being a bright-white glow, ceasing on the plant becoming dry; one, growing on a palm in Brazil, and hence called by the inhabitants the "Flor de coca"—gives out a pale greenish-hued light.[3] Decaying wood is often luminous from the mycelium of fungi creeping through its tissues.

Tulasne[4] examined the luminosity of the Agaric of the olive without being able to explain it; but Fabre, in a paper in the same journal, ascribes it to a temporary increase of oxidation.

Luminosity of Sap.—The sap of some plants is also luminous. Mornay describes a tree in South America called "Cipo de Cunaman," with a milky juice, which gives out in the dark a bright light. Martius also mentions that when *Euphorbia phosphorea* was wounded, the sap gave out a light. The same celebrated traveller and botanist refers to the observations of Senebier, who found that when an *Arum* was confined in oxygen gas, it gave out light as well as heat. The whole subject still requires investigation. In the majority of cases it is probably due to increased oxidation in the tissues of the plant, though sometimes, as in *Dictamnus*, a volatile oil may be the cause.[5]

---

[1] Gardeners' Chronicle, Sept. 21, 1872; with remarks of W. G. Smith in No. for Sept. 28.—Grevillea, i. 75. See also Gardeners' Chronicle, 1872, p. 1327, and 1874, p. 63.

[2] Hooker's Journal of Botany, April 1842.

[3] Gardner in Hooker's Journ of Bot., ii. 426.

[4] Ann. des Sc. Nat., 1848, ix. 338.

[5] For a good summary—for which we are indebted for some of the foregoing facts—see Science Gossip, 1871, p. 121; and Gardeners' Chronicle, 1871, p. 904. A tolerably complete bibliography of writings will be found in Schleiden's Principles, p. 542; or in Meyen's Physiologie, Bd. ii. 192.

TEMPERATURE OF PLANTS.

Though at the time of the flow of the sap the general temperature of the tissues of the plant may be slightly raised, the range of heat is not great, and bears a tolerably exact ratio to the ordinary temperature of the surrounding atmosphere, soil, and fluid absorbed. However, at the period of flowering, the temperature within the flower is much elevated. This is chiefly observed in the order Araceæ. As early as 1777, Lamarck made observations on *Arum Italicum*, Mill.; and subsequently these observations were repeated by Senebier on the common cuckoo-pint (*Arum maculatum*), with a result which showed that at the period of flowering there was heat 9° above the atmosphere. Hubert, on placing a thermometer in the centre of several flowering specimens of *Arum cordifolium*, found it elevated 25° above the temperature of the air at the surface of the ground. Planchon found a thermometer thrust into the flower of *Victoria regia*, a water-plant, showed 6° above the temperature of the air. Similar observations have been made by Saussure, Schultz, De Vriese, Vrolik, Treviranus, Gärtner, Brongniart, Göppert, Warming of Copenhagen, and others. The last-named botanist made his observations on a Brazilian species of *Philodendron—P. Lundii*, Wrmg. He found that there was a series of calorific undulations which did not coincide with the time when the heat of the air was greatest. The greatest heat which Dr Warming observed was 39½° Cent., showing a difference of 18½° between the temperature of the flower and the surrounding air.[1]

The cause of this increase of temperature is probably an increased absorption of oxygen, and formation of a large quantity of carbonic acid, which has also the effect of increasing the volume of the flowers.[2]

It has also been long known that seed when germinating, as they lie heaped in masses, as on a malting-floor, evolve a considerable amount of heat, this evolution of heat not being connected, as Göppert showed, with fermentation, but with germination. Seeds of hemp, clover, *Spergula*, *Brassica*, &c.—all of different chemical composition—when germinating in quantities of about

---

[1] Vidensk. Medd. fra den Naturhistoriske Forening i Kjöb, 1869. See also Dutrochet, Comptes rendus, 1839, p. 695; Brongniart, Nouv. Ann. de Muséum, iii.; Vrolik and De Vriese, Ann. des Sc. Nat., ser. 2, v. 134, and xi. 62; Van Beek and Bersgma, Obs. thermoelect. sur l'élévation de temperature des fleurs de Colocasia odorata, 1838; Pfeffer, Sitzungsbericht, d. ges. z. Beförderung d. ges. Naturwissensch. z. Marburg, 6th Feb. 1863, &c.

[2] Rameux in Ann. des Sc. Nat., 1843; Schübler in Poggendorff's Annalen, x.; Dutrochet, Ann. Sc. Nat. (ser. 2), t. xii.; Gardner in Trans. Linn. Soc., 1841, and Phil. Mag., 1842; and op. cit., *ut supra*.

a pound weight, become heated, when the surrounding atmosphere is at a temperature of 48°-66° to 59°-120° Fahr. Full-grown plants, when heaped on the floor and covered with bad conductors of heat, cause a rise of a thermometer placed among them of about from 2°-7°, and even (as in the case of *Spergula*) as much as 22° above the temperature of the air. Indeed, plants standing alone show an evolution of heat from one-sixth to one-twelfth of a degree above the air.[1]

All these manifestations of increased temperature in germinating seed probably point to an increased consumption of oxygen, and exhalation of carbonic acid. In vegetating organs, Mohl considers the source of heat different. "It is true," he says, "that oxygen is consumed and carbonic acid formed by all organs; but since, on the whole, a greater quantity of carbonic acid is decomposed in the green-coloured organs than is formed in the remaining parts, more heat must be consumed than produced in the respiratory process of vegetating organs. But the evolution of heat must be connected with the nutrient process; for the plant forms its organic substance, if not wholly yet in great part, from gases and liquids. Since, then, the growth of the plant exhibits a daily exaltation, occurring about noon, it is quite in accordance that the evolution of heat also should occur in increased degree at the same time." This seems reasonable.

The experiments made regarding the temperature of trees by boring holes in them, and inserting long-tubed thermometers, are contradictory, owing to many disturbing causes of error. Yet the rule is, that their temperature is higher in the winter and lower in the summer in the tree than in the surrounding atmosphere. Wood in its longitudinal direction is a good, but across its fibres it is a bad, conductor of heat.[2]

VEGETABLE NOSOLOGY AND TERATOLOGY.

Vegetable nosology, or the diseases to which plants are subject, is a long and intricate subject. Fortunately, however, it does not

---

[1] Dutrochet in Ann. des Sc. Nat., ii. 77 (1839).

[2] See Schleiden's Principles, p. 541; Meyen's Physiologie, Bd. ii. 164; Halder, Beobrachtungen über die Temperatur der Vegetabilien, 1826; Neuffer, Untersuch. über die Temperaturer underungen der Vegetabilien, 1829; De la Rive and De Candolle's Poggendorff's Annalen, Bd. xiv. s. 590; Sachs' Handbuche, s. 48 *et seq.*: (for many original observations) Flora, 1864, s. 5; and Jahrb. f. wiss. botan., ii. (1868) 328; Villari Poggendorff's Annalen, 1868, Bd. 133, s. 412; De Vriese, Archives Néerlandaises, t. v. (1870); De Candolle in Biblioth. Universelle, 1863; Koppen, Wärme und Pflanzenwachsthum, 1870 (*teste* Sachs); Göppert, Bot. Zeit., 1871, Nos. 4 and 5; and Bibliog. in Sachs' Lehrbuch, ed. 1873 ("Allgemeine Lebensbedingungen der Pflanzen," s. 632 *et seq.*)

call for discussion in a work of this kind, coming under the department of horticulture and arboriculture; and therefore, though a legitimate subject of study by the scientific botanist, is not yet a part of botanical science, any more than is the cultivation and conservation of living plants. Disease may be defined as that state of the organism in which all the organs are not performing their functions in accordance with nature. The causes of these diseased conditions in plants may be classed as follows: 1. Parasitic fungi and other plants, such as dodder attacking the tissues. 2. Insects causing galls and fissures in the leaves and bark, as well as wounds of any description. 3. Poisonous gases in the air or soil, as well as any poisonous material so placed as to affect the nutrition. 4. Atmospheric or other conditions, so affecting the plant as to alter the conditions of nutrition by giving a redundancy or deficiency of air, light, moisture, warmth, &c. Under these four heads most of the diseases of plants find a place.

Vegetable *Teratology* is that portion of the subject which takes cognisance of deformities and abnormalities of growth, and is not properly disease any more than abnormalities in the animal organism are; nor, when such abnormalities do not injuriously affect the reproductive or nutritive powers of the plant, are they productive of disease. These teratological variations we have noted, so far as was necessary, while studying the normal conditions of the organs affected.[1]

With Masters, we may divide the phenomena of teratology into four sections: 1. Deviation from the ordinary arrangement, comprising (α) *union of parts* (cohesion and adhesion); (β) *independence of organs* (fission, dialysis, solution); (γ) *alteration of position* (displacement, prolification, heterotaxy, heterogamy (p. 407, 418), alteration in the direction of organs). 2. Deviations from ordinary forms, comprising (α) strasimorphy (persistence of juvenile forms); (β) pleiomorphy (irregular peloria); (γ) metamorphy (phyllody, metamorphy of the floral organs); (δ) heteromorphy (deformities, polymorphy, alteration of colours). 3. Deviations from ordinary number,—(α) increase of number of organs (multiplication of axile organs, inflorescence, multiplication of foliar organs); (β) diminished number of organs (suppression of axile organs, suppression of foliar organs). 4. Deviations from ordinary size and consistence,—(α) hypertrophy (enlargement, elongation, enation); (β) atrophy (abortion, degeneration).

[1] There are various works treating of this subject; but the most recent, as well as the ablest and most exhaustive, is Dr Maxwell Masters's Vegetable Teratology (Ray Society, 1869), to which the student is referred.

INDEX AND GLOSSARY.

EDUCATIONAL WORKS

PUBLISHED BY

WILLIAM BLACKWOOD & SONS,

EDINBURGH AND LONDON.

◆

English Language.

AN ETYMOLOGICAL AND PRONOUNCING DICTIONARY OF THE ENGLISH LANGUAGE. Including a very copious selection of Scientific, Technical, and other Terms and Phrases. Designed for use in Schools and Colleges, and as a Handy Book for General Reference. By the Rev. JAMES STORMONTH, and the Rev. P. H. PHELP, M.A. Crown 8vo, pp. 760, 7s. 6d.

THE SCHOOL ETYMOLOGICAL DICTIONARY AND WORD-BOOK. Combining the advantages of an ordinary Pronouncing School Dictionary and an Etymological Spelling-Book. By the Rev. JAMES STORMONTH. Fcap. 8vo, pp. 254, 2s.

ENGLISH PROSE COMPOSITION: A PRACTICAL MANUAL FOR USE IN SCHOOLS. By JAMES CURRIE, M.A., Principal of the Church of Scotland Training College, Edinburgh. Ninth Edition, 1s. 6d.

"We do not remember having seen a work so completely to our mind as this, which combines sound theory with judicious practice. Proceeding step by step, it advances from the formation of the shortest sentences to the composition of complete essays, the pupil being everywhere furnished with all needful assistance in the way of models and hints. Nobody can work through such a book as this without thoroughly understanding the structure of sentences, and acquiring facility in arranging and expressing his thoughts appropriately. It ought to be extensively used."—*Athenæum.*

A MANUAL OF ENGLISH PROSE LITERATURE, Biographical and Critical: designed mainly to show characteristics of style. By W. MINTO, M.A. Crown 8vo, 10s. 6d.

"Is a work which all who desire to make a close study of style in English prose will do well to use attentively."—*Standard.*

"Here we do not find the *crambe repetita* of old critical formulæ, the simple echoes of superannuated rhetorical dicta, but a close and careful analysis of the main attributes of style, as developed in the work of its greatest masters, stated with remarkable clearness of expression, and arranged upon a plan of most exact method. Nothing can be well conceived more consummate as a matter of skill than the analytical processes of the writer as he lays bare to our view the whole anatomy—even every joint and sinew and artery in the framework—of the sentence he dissects, and as he points out their reciprocal relations, their minute interdependencies."—*School Board Chronicle.*

"An admirable book, well selected and well put together."—*Westminster Review.*

PROGRESSIVE AND CLASSIFIED SPELLING-BOOK. By HANNAH R. LOCKWOOD, Authoress of 'Little Mary's Mythology.' Fcap. 8vo, 1s. 6d.

Geography.

NEW AND GREATLY IMPROVED EDITION.

A MANUAL OF MODERN GEOGRAPHY, MATHEMATICAL, PHYSICAL, AND POLITICAL. By the Rev. ALEXANDER MACKAY, LL.D., F.R.G.S. Crown 8vo, pp. 676. 7s. 6d.

This volume—the result of many years' unremitting application—is specially adapted for the use of Teachers, Advanced Classes, Candidates for the Civil Service, and proficients in geography generally.

TWENTY-FOURTH THOUSAND.

ELEMENTS OF MODERN GEOGRAPHY. By the Same. Thirteenth Edition, revised to the present time. Crown 8vo, pp. 300. 3s.

The 'Elements' form a careful condensation of the 'Manual,' the order of arrangement being the same, the river-systems of the globe playing the same conspicuous part, the pronunciation being given, and the results of the latest census being uniformly exhibited. This volume is now extensively introduced into many of the best schools in the kingdom.

SIXTY-SECOND THOUSAND.

OUTLINES OF MODERN GEOGRAPHY: FIFTEENTH EDITION, REVISED TO THE PRESENT TIME. By the Same. 18mo, pp. 112. 1s.

These 'Outlines'—in many respects an epitome of the 'Elements'—are carefully prepared to meet the wants of beginners. The arrangement is the same as in the Author's larger works. Minute details are avoided, the broad outlines are graphically presented, the accentuation marked, and the most recent changes in political geography exhibited.

FORTY-FIRST THOUSAND, REVISED TO THE PRESENT TIME.

FIRST STEPS IN GEOGRAPHY. By the Same. 18mo, pp. 56. Sewed, 4d. In cloth, 6d.

GEOGRAPHY OF THE BRITISH EMPIRE. From 'First Steps in Geography.' By the Same. 3d.

Agriculture.

CATECHISM OF PRACTICAL AGRICULTURE. By HENRY STEPHENS, F.R.S.E., Author of the 'Book of the Farm.' A New Edition. With Engravings. 1s.

PROFESSOR JOHNSTON'S CATECHISM OF AGRICULTURAL CHEMISTRY. A New Edition, edited by Professor VOELCKER. With Engravings. 1s.

PROFESSOR JOHNSTON'S ELEMENTS OF AGRICULTURAL CHEMISTRY AND GEOLOGY. A New Edition, revised and brought down to the present time, by G. T. ATKINSON, B.A., F.C.S., Clifton College. Foolscap, 6s. 6d.

Geographical Class-Books.

OPINIONS OF DR MACKAY'S SERIES.

MANUAL.

Annual Address of the President of the Royal Geographical Society (Sir Roderick I. Murchison).—We must admire the ability and persevering research with which he has succeeded in imparting to his 'Manual' so much freshness and originality. In no respect is this character more apparent than in the plan of arrangement, by which the author commences his description of the physical geography of each tract by a sketch of its true basis or geological structure. The work is largely sold in Scotland, but has not been sufficiently spoken of in England. It is, indeed, a most useful school-book in opening out geographical knowledge.

Saturday Review.—It contains a prodigious array of geographical facts, and will be found useful for reference.

English Journal of Education.—Of all the Manuals on Geography that have come under our notice, we place the one whose title is given above in the first rank. For fulness of information, for knowledge of method in arrangement, for the manner in which the details are handled, we know of no work that can, in these respects, compete with Mr Mackay's Manual.

ELEMENTS.

A. KEITH JOHNSTON, LL.D., F.R.S.E., F.R.G.S., H.M. Geographer for Scotland, Author of the 'Physical Atlas,' &c. &c.—There is no work of the kind in this or any other language, known to me, which comes so near my *ideal* of perfection in a school-book, on the important subject of which it treats. In arrangement, style, selection of matter, clearness, and thorough accuracy of statement, it is without a rival; and knowing, as I do, the vast amount of labour and research you bestowed on its production, I trust it will be so appreciated as to insure, by an extensive sale, a well-merited reward.

G. BICKERTON, Esq., Edinburgh Institution.—I have been led to form a very high opinion of Mackay's 'Manual of Geography' and 'Elements of Geography,' partly from a careful examination of them, and partly from my experience of the latter as a text-book in the EDINBURGH INSTITUTION. One of their most valuable features is the elaborate Table of River-Basins and Towns, which is given in addition to the ordinary Province or County list, so that a good idea may be obtained by the pupil of the natural as well as the political relationship of the towns in each country. On all matters connected with Physical Geography, Ethnography, Government, &c., the information is full, accurate, and well digested. They are books that can be strongly recommended to the student of geography.

RICHARD D. GRAHAM, English Master, College for Daughters of Ministers of the Church of Scotland and of Professors in the Scottish Universities.—No work with which I am acquainted so amply fulfils the conditions of a perfect text-book on the important subject of which it treats, as Dr Mackay's 'Elements of Modern Geography.' In fulness and accuracy of details, in the scientific grouping of facts, combined with clearness and simplicity of statement, it stands alone, and leaves almost nothing to be desired in the way of improvement. Eminently fitted, by reason of this exceptional variety and thoroughness, to meet all the requirements of higher education, it is never without a living interest, which adapts it to the intelligence of ordinary pupils. It is not the least of its merits that its information is abreast of all the latest developments in geographical science, accurately exhibiting both the recent political and territorial changes in Europe, and the many important results of modern travel and research.

Spectator.—The best Geography we have ever met with.

Geology.

"*Few of our handbooks of popular science can be said to have greater or more decisive merit than those of Mr Page on Geology and Palæontology. They are clear and vigorous in style, they never oppress the reader with a pedantic display of learning, nor overwhelm him with a pompous and superfluous terminology; and they have the happy art of taking him straightway to the face of nature herself, instead of leading him by the tortuous and bewildering paths of technical system and artificial classification.*"—Saturday Review.

INTRODUCTORY TEXT-BOOK OF GEOLOGY. By DAVID PAGE, LL.D., Professor of Geology in the Durham University of Physical Science, Newcastle. With Engravings on Wood and Glossarial Index. Tenth Edition. 2s. 6d.

"It has not been our good fortune to examine a text-book on science of which we could express an opinion so entirely favourable as we are enabled to do of Mr Page's little work."—*Athenæum.*

ADVANCED TEXT-BOOK OF GEOLOGY, DESCRIPTIVE AND INDUSTRIAL. By the Same. With Engravings, and Glossary of Scientific Terms. Fifth Edition, revised and enlarged. 7s. 6d.

"We have carefully read this truly satisfactory book, and do not hesitate to say that it is an excellent compendium of the great facts of Geology, and written in a truthful and philosophic spirit."—*Edinburgh Philosophical Journal.*

"As a school-book nothing can match the Advanced Text-Book of Geology by Professor Page of Newcastle."—*Mechanics' Magazine.*

"We know of no introduction containing a larger amount of information in the same space, and which we could more cordially recommend to the geological student."—*Athenæum.*

THE GEOLOGICAL EXAMINATOR. A Progressive Series of Questions, adapted to the Introductory and Advanced Text-Books of Geology. Prepared to assist Teachers in framing their Examinations, and Students in testing their own Progress and Proficiency. By the Same. Fifth Edition. 9d.

SYNOPSES OF SUBJECTS TAUGHT IN THE GEOLOGICAL CLASS, College of Physical Science, Newcastle-on-Tyne, University of Durham. By the Same. Fcap., cloth, 2s. 6d.

THE CRUST OF THE EARTH: A HANDY OUTLINE OF GEOLOGY. By the Same. Sixth Edition. 1s.

"An eminently satisfactory work, giving, in less than 100 pages, an admirable outline sketch of Geology, . . . forming, if not a royal road, at least one of the smoothest we possess to an intelligent acquaintance with geological phenomena."—*Scotsman.*

"Of singular merit for its clearness and trustworthy character."—*Standard.*

GEOLOGY FOR GENERAL READERS. A Series of Popular Sketches in Geology and Palæontology. By the Same. Third Edition, enlarged. 6s.

"This is one of the best of Mr Page's many good books. It is written in a flowing popular style. Without illustration or any extraneous aid, the narrative must prove attractive to any intelligent reader."—*Geological Magazine.*

HANDBOOK OF GEOLOGICAL TERMS, GEOLOGY, AND PHYSICAL GEOGRAPHY. By the Same. Second Edition, enlarged. 7s. 6d.

"The only dictionary of Geology in the English language—modern in date, and exhaustive in treatment."—*Review.*

CHIPS AND CHAPTERS. A Book for Amateurs and Young Geologists. By the Same. 5s.

THE PAST AND PRESENT LIFE OF THE GLOBE. With numerous Illustrations. By the Same. Crown 8vo. 6s.

THE PHILOSOPHY OF GEOLOGY. A Brief Review of the Aim, Scope, and Character of Geological Inquiry. By the Same. Fcap. 8vo. 3s. 6d.

"The great value of Mr Page's volume is its suggestive character. The problems he discusses are the highest and most interesting in the science—those on which it most becomes the thinkers and the leaders of the age to make up their minds. The time is now past for geologists to observe silence on these matters, and in this way to depreciate at once the interest and importance of their investigations. It is well to know that, however they may decide, questions of high philosophy are at stake, and therefore we give a hearty welcome to every book which, like Mr Page's, discusses these questions in a fair and liberal spirit."—*Scotsman.*

Physical Geography.

INTRODUCTORY TEXT-BOOK OF PHYSICAL GEOGRAPHY. With Sketch-Maps and Illustrations. By DAVID PAGE, LL.D., Professor of Geology in the Durham University of Physical Science, Newcastle. Sixth Edition. 2s. 6d.

"The divisions of the subject are so clearly defined, the explanations are so lucid, the relations of one portion of the subject to another are so satisfactorily shown, and, above all, the bearings of the allied sciences to Physical Geography are brought out with so much precision, that every reader will feel that difficulties have been removed, and the path of study smoothed before him."—*Athenæum.*

"Whether as a school-book or a manual for the private student, this work has no equal in our Educational literature."—*Iron.*

ADVANCED TEXT-BOOK OF PHYSICAL GEOGRAPHY. By the Same. With Engravings. Second Edition. 5s.

"A thoroughly good Text-Book of Physical Geography."—*Saturday Review.*

"It is not often our good fortune to meet with scientific manuals so cheap and so excellent in matter, and so useful for the practical purposes of education, as this admirable work, which is beyond all question the best of its kind."—*Evening Standard.*

EXAMINATIONS ON PHYSICAL GEOGRAPHY. A Progressive Series of Questions, adapted to the Introductory and Advanced Text-Books of Physical Geography. By the Same. Second Edition. 9d.

COMPARATIVE GEOGRAPHY. By CARL RITTER. Translated by W. L. GAGE. Fcap., 3s. 6d.

Zoology.

OUTLINES OF NATURAL HISTORY, for Beginners; being Descriptions of a Progressive Series of Zoological Types. By HENRY ALLEYNE NICHOLSON, M.D., F.R.S.E., F.G.S., &c., Professor of Zoology in the Royal College of Science, Dublin. 52 Engravings, 1s. 6d.

"There has been no book since Patterson's well known 'Zoology for Schools' that has so completely provided for the class to which it is addressed as the capital little volume by Dr Nicholson."—*Popular Science Review.*

BY THE SAME AUTHOR.

INTRODUCTORY TEXT-BOOK OF ZOOLOGY, FOR THE USE OF JUNIOR CLASSES. With 127 Engravings. A New Edition, 2s. 6d.

"Very suitable for junior classes in schools. There is no reason why any one should not become acquainted with the principles of the science, and the facts on which they are based, as set forth in this volume."—*Lancet.*

"Nothing can be better adapted to its object than this cheap and well-written Introduction."—*London Quarterly Review.*

TEXT-BOOK OF ZOOLOGY, FOR THE USE OF SCHOOLS. Second Edition, enlarged. Crown 8vo, with 188 Engravings on Wood, 6s.

"This capital introduction to natural history is illustrated and well got up in every way. We should be glad to see it generally used in schools."—*Medical Press and Circular.*

A MANUAL OF ZOOLOGY, FOR THE USE OF STUDENTS. With a General Introduction on the Principles of Zoology. Third Edition. Crown 8vo, pp. 706, with 280 Engravings on Wood, 12s. 6d.

"It is the best manual of zoology yet published, not merely in England, but in Europe."—*Pall Mall Gazette, July* 20, 1871.

"The best treatise on Zoology in moderate compass that we possess."—*Lancet, May* 18, 1872.

A MANUAL OF PALÆONTOLOGY, FOR THE USE OF STUDENTS. With a General Introduction on the Principles of Palæontology. Crown 8vo, with upwards of 400 Engravings, 15s.

"This book will be found to be one of the best of guides to the principles of Palæontology and the study of organic remains."—*Athenæum.*

INTRODUCTION TO THE STUDY OF BIOLOGY. Crown 8vo, with numerous Engravings, 5s.

EXAMINATIONS IN NATURAL HISTORY; being a Progressive Series of Questions adapted to the Author's Introductory and Advanced Text-Books and the Student's Manual of Zoology. 1s.

History.

EPITOME OF ALISON'S HISTORY OF EUROPE, FOR THE USE OF SCHOOLS. Sixteenth Edition. Post 8vo, pp. 604. 7s. 6d. bound in leather.

ATLAS TO EPITOME OF THE HISTORY OF EUROPE. ELEVEN COLOURED MAPS. By A. KEITH JOHNSTON, LL.D., F.R.S.E. In 4to, 7s.

THE EIGHTEEN CHRISTIAN CENTURIES. By the Rev. JAMES WHITE, Author of 'The History of France.' Seventh Edition, post 8vo, with Index, 6s.

"He goes to work upon the only true principle, and produces a picture that at once satisfies truth, arrests the memory, and fills the imagination. It will be difficult to lay hands on any book of the kind more useful and more entertaining."—*Times.*

"He has seized the salient points—indeed, the governing incidents—in each century, and shown their received bearing as well on their own age as on the progress of the world. Vigorously and briefly, often by a single touch, has he marked the traits of leading men; when needful, he touches slightly their biographical career. The state of the country and of society, of arts and learning, and, more than all, of the modes of living, are graphically sketched, and, upon the whole, with more fulness than any other division."—*Spectator.*

HISTORY OF FRANCE, FROM THE EARLIEST TIMES. By the Rev. JAMES WHITE, Author of 'The Eighteen Christian Centuries.' Fifth Edition, post 8vo, with Index, 6s.

"An excellent and comprehensive compendium of French history."—*National Review.*

FACTS AND DATES; or, The Leading Events in Sacred and Profane History, and the Principal Facts in the Various Physical Sciences: the Memory being aided throughout by a Simple and Natural Method. For Schools and Private Reference. By the Rev. ALEX. MACKAY, LL.D., F.R.G.S., Author of 'A Manual of Modern Geography,' &c. Second Edition, crown 8vo, pp. 336. 4s.

THE LIFE AND LABOURS OF THE APOSTLE PAUL. A continuous Narrative for Schools and Bible Classes. By CHARLES MICHIE, M.A. Fcap. 8vo, cloth, 1s.

"The details are carefully collected and skilfully put together, and the outcome is a succinct, yet clear and comprehensive, view of the life and labours of the great Apostle. The story of Paul's life, so replete with spirit-stirring incidents, is told in a manner extremely well fitted to arrest the attention of advanced pupils, and we can with confidence commend this little work as an admirable text-book for Bible-classes. The narrative is enriched by footnotes, from which it is apparent that Mr Michie is well posted up in the literature of the subject. These are subjoined without any pretence or parade of learning, and only when required to elucidate or illustrate the text. The map at the close will enable the reader to trace the course of the Apostle in his various missionary tours. We give this handbook our warm commendation: it certainly deserves a wide circulation."—*National Education Gazette.*

IMPROVED EDITIONS.

School Atlases.

BY A. KEITH JOHNSTON, LL.D., &c.
Author of the Royal and the Physical Atlases, &c.

ATLAS OF GENERAL AND DESCRIPTIVE GEOGRAPHY. A New and Enlarged Edition, suited to the best Text-Books; with Geographical information brought up to the time of publication. 26 Maps, clearly and uniformly printed in colours, with Index. Imp. 8vo. Half-bound, 12s. 6d.

ATLAS OF PHYSICAL GEOGRAPHY, illustrating, in a Series of Original Designs, the Elementary Facts of GEOLOGY, HYDROGRAPHY, METEOROLOGY, and NATURAL HISTORY. A New and Enlarged Edition, containing 4 new Maps and Letter-press. 20 Coloured Maps. Imp. 8vo. Half-bound, 12s. 6d.

ATLAS OF ASTRONOMY. A New and Enlarged Edition, 21 Coloured Plates. With an Elementary Survey of the Heavens, designed as an accompaniment to this Atlas, by ROBERT GRANT, LL.D., &c., Professor of Astronomy and Director of the Observatory in the University of Glasgow. Imp. 8vo. Half-bound, 12s. 6d.

ATLAS OF CLASSICAL GEOGRAPHY. A New and Enlarged Edition. Constructed from the best materials, and embodying the results of the most recent investigations, accompanied by a complete INDEX OF PLACES, in which the proper quantities are given by T. HARVEY and E. WORSLEY, MM.A. Oxon. 21 Coloured Maps. Imp. 8vo. Half-bound, 12s. 6d.

"This Edition is so much enlarged and improved as to be virtually a new work, surpassing everything else of the kind extant, both in utility and beauty."
—*Athenæum.*

ELEMENTARY ATLAS OF GENERAL AND DESCRIPTIVE GEOGRAPHY, for the Use of Junior Classes; including a MAP OF CANAAN and PALESTINE, with GENERAL INDEX. 8vo, half-bound, 5s.

NEW ATLAS FOR PUPIL-TEACHERS.

THE HANDY ROYAL ATLAS. 46 Maps clearly printed and carefully coloured, with GENERAL INDEX. Imp. 4to, £2, 12s. 6d., half-bound morocco. A New Edition, brought up to the present time.

This work has been constructed for the purpose of placing in the hands of the public a useful and thoroughly accurate ATLAS of Maps of Modern Geography, in a convenient form, and at a moderate price. It is based on the 'ROYAL ATLAS,' by the same Author; and, in so far as the scale permits, it comprises many of the excellences which its prototype is acknowledged to possess. The aim has been to make the book strictly what its name implies, a HANDY ATLAS--a valuable substitute for the 'Royal,' where that is too bulky or too expensive to find a place, a needful auxiliary to the junior branches of families, and a *vade mecum* to the tutor and the pupil-teacher.

Keith Johnston's Atlases.

EXTRACTS FROM OPINIONS OF THE PRESS.

SCHOOL ATLASES.

"They are as superior to all School Atlases within our knowledge, as were the larger works of the same Author in advance of those that preceded them."—*Educational Times.*

"Decidedly the best School Atlases we have ever seen."—*English Journal of Education.*

" . . . The 'Physical Atlas' seems to us particularly well executed. . . . The last generation had no such help to learning as is afforded in these excellent elementary Maps. The 'Classical Atlas' is a great improvement on what has usually gone by that name; not only is it fuller, but in some cases it gives the same country more than once in different periods of time. Thus it approaches the special value of a historical atlas. The 'General Atlas' is wonderfully full and accurate for its scale. . . . Finally, the 'Astronomical Atlas,' in which Mr Hind is responsible for the scientific accuracy of the maps, supplies an admitted educational want. No better companion to an elementary astronomical treatise could be found than this cheap and convenient collection of maps."—*Saturday Review.*

"The plan of these Atlases is admirable, and the excellence of the plan is rivalled by the beauty of the execution. . . . The best security for the accuracy and substantial value of a School Atlas is to have it from the hands of a man like our Author, who has perfected his skill by the execution of much larger works, and gained a character which he will be careful not to jeopardise by attaching his name to anything that is crude, slovenly, or superficial."—*Scotsman.*

"This Edition of the 'Classical Atlas' is so much enlarged and improved as to be virtually a new work, surpassing everything else of the kind extant, both in utility and beauty."—*Athenæum.*

THE HANDY ROYAL ATLAS.

"Is probably the best work of the kind now published."—*Times.*

"Not only are the present territorial adjustments duly registered in all these Maps, but the latest discoveries in Central Asia, in Africa, and America, have been delineated with laborious fidelity. Indeed the ample illustration of recent discovery, and of the great groups of dependencies on the British Crown, renders Dr Johnston's the best of all Atlases for English use."—*Pall Mall Gazette.*

"This is Mr Keith Johnston's admirable Royal Atlas diminished in bulk and scale so as to be, perhaps, fairly entitled to the name of 'Handy,' but still not so much diminished but what it constitutes an accurate and useful general Atlas for ordinary households."—*Spectator.*

"The 'Handy Atlas' is thoroughly deserving of its name. Not only does it contain the latest information, but its size and arrangement render it perfect as a book of reference."—*Standard.*

Arithmetic.

THE THEORY OF ARITHMETIC. By David Munn, F.R.S.E., Mathematical Master, Royal High School of Edinburgh. Crown 8vo, pp. 294. 5s.

"We want books of this kind very much—books which aim at developing the educational value of Arithmetic by showing how admirably it is calculated to exercise the thinking powers of the young. Your book is, I think, excellent—brief, but clear; and I look forward to the good effects which it shall produce, in awaking the minds of many who regard Arithmetic as a mere mechanical process."—*Professor Kelland.*

ELEMENTARY ARITHMETIC. By Edward Sang, F.R.S.E. This Treatise is intended to supply the great desideratum of an intellectual instead of a routine course of instruction in Arithmetic. Post 8vo, 5s.

THE HIGHER ARITHMETIC. By the same Author. Being a Sequel to 'Elementary Arithmetic.' Crown 8vo, 5s.

FIVE-PLACE LOGARITHMS. Arranged by E. Sang, F.R.S.E. Sixpence. For the Waistcoat-Pocket.

TREATISE ON ARITHMETIC, with numerous Exercises for Teaching in Classes. By James Watson, one of the Masters of Heriot's Hospital. Foolscap, 1s.

IN THE PRESS.

New Books.

ADVANCED TEXT-BOOK OF BOTANY. For the Use of Students. By Robert Brown, M.A., Ph.D., F.R.G.S., Lecturer on Botany under the Science and Art Department of the Committee of the Privy Council on Education.

CHARACTERISTICS OF ENGLISH POETS, from Chaucer to Shirley. By Wm. Minto, M.A., Author of 'A Manual of English Prose Literature.' One vol. crown 8vo.

A COURSE OF HISTORICAL STUDY, for the use of Schools and for Private Reading. In Three Parts, comprising—Ancient History, Middle Ages, Modern History. By Mademoiselle Reynaud.

THE HANDY SCHOOL DICTIONARY, Pronouncing and Explanatory. Also containing Lists of Prefixes and Postfixes; Rules for Spelling correctly; Words same in Sound but different in Spelling and Meaning; Common Abbreviations; and Common Quotations from the Latin, French, &c. For Use in Elementary Schools. By the Rev. James Stormonth, Author of 'The Etymological and Pronouncing Dictionary of the English Language,' 'The School Etymological Dictionary,' &c.

Miscellaneous.

A TREASURY OF THE ENGLISH AND GERMAN LANGUAGES. Compiled from the best Authors and Lexicographers in both Languages. Adapted to the Use of Schools, Students, Travellers, and Men of Business; and forming a Companion to all German-English Dictionaries. By JOSEPH CAUVIN, LL.D. & PH.D., of the University of Göttingen, &c. Crown 8vo, 7s. 6d., bound in cloth.

"An excellent English-German Dictionary, which supplies a real want."—*Saturday Review.*

"The difficulty of translating English into German may be greatly alleviated by the use of this copious and excellent English-German Dictionary, which specifies the different senses of each English word, and gives suitable German equivalents. It also supplies an abundance of idiomatic phraseology, with many passages from Shakespeare and other authors aptly rendered in German. Compared with other dictionaries, it has decidedly the advantage."—*Athenæum.*

INTRODUCTORY TEXT-BOOK OF METEOROLOGY. By ALEXANDER BUCHAN, M.A., F.R.S.E., Secretary of the Scottish Meteorological Society, Author of 'Handy Book of Meteorology,' &c. Crown 8vo, with 8 Coloured Charts and other Engravings, pp. 218. 4s. 6d.

"A handy compendium of Meteorology by one of the most competent authorities on this branch of science."—*Petermann's Geographische Mittheilungen.*

"We can recommend it as a handy, clear, and scientific introduction to the theory of Meteorology, written by a man who has evidently mastered his subject."—*Lancet.*

"An exceedingly useful volume."—*Athenæum.*

A GLOSSARY OF NAVIGATION. Containing the Definitions and Propositions of the Science, Explanation of Terms, and Description of Instruments. By the Rev. J. B. HARBORD, M.A., Assistant Director of Education, Admiralty. Crown 8vo, Illustrated with Diagrams, 6s.

DEFINITIONS AND DIAGRAMS IN ASTRONOMY AND NAVIGATION. By the Same. 1s. 6d.

ELEMENTARY HANDBOOK OF PHYSICS. With 210 Diagrams. By WILLIAM ROSSITER, F.R.A.S., &c. Crown 8vo, pp. 390. 5s.

"A singularly interesting Treatise on Physics, founded on facts and phenomena gained at first hand by the Author, and expounded in a style which is a model of that simplicity and ease in writing which betokens mastery of the subject. To those who require a non-mathematical exposition of the principles of Physics a better book cannot be recommended."—*Pall Mall Gazette.*

Crown 8vo, pp. 760, 7s. 6d.,

AN ETYMOLOGICAL AND PRONOUNCING DICTIONARY OF THE ENGLISH LANGUAGE.

INCLUDING A VERY COPIOUS SELECTION OF
SCIENTIFIC, TECHNICAL, AND OTHER TERMS AND PHRASES.
DESIGNED FOR USE IN SCHOOLS AND COLLEGES,
AND AS
A HANDY BOOK FOR GENERAL REFERENCE.

BY THE REV. JAMES STORMONTH,
AND THE
REV. P. H. PHELP, M.A.

OPINIONS OF THE PRESS.

"This will be found a most admirable and useful Dictionary by the student, the man of business, or the general inquirer. Its design is to supply a full and complete pronouncing etymological, and explanatory Dictionary of the English language; and, as far as we can judge, in that design it most completely succeeds. It contains an unusual number of scientific names and terms, English phrases, and familiar colloquialisms; this will considerably enhance its value to the general searcher after information. The author seems to us to have planned the Dictionary exceedingly well. The Dictionary words are printed in bold black type, and in single letters, that being the form in which words are usually presented to the reader. Capital letters begin such words only in proper names, and others which are always so printed. They are grouped under a leading word, from which they may be presumed naturally to fall or be formed, or singly follow in alphabetical order—only so, however, when they are derived from the same leading root, and when the alphabetical order may not be materially disturbed. The roots are enclosed within brackets, and for them the works of the best and most recent authorities seem to have been consulted. The meanings are those usually given, but they have been simplified as much as possible. Nothing unnecessary is given; but, in the way of definition, there will be found a vast quantity of new matter. The phonetic spelling of the words has been carefully revised by a Cambridge graduate—Mr Phelp; and Dr Page, the well-known geologist, has attended to the correctness of the various scientific terms in the book. The Dictionary altogether is very complete."—*Greenock Advertiser.*

"This Dictionary is admirable. The etymological part especially is good and sound. We have turned to 'calamity,' 'forest,' 'poltroon,' and a number of other crucial words, and find them all derived according to the newest lights. There is nothing about 'calamus,' and foris,' and 'pollice truncus,' such as we used in the etymological dictionaries of the old type. The work deserves a place in every English School, whether boys' or girls'."—*Westminster Review.*

OPINIONS—*continued.*

"That which is now before us is evidently a work on which enormous pains have been bestowed. The compilation and arrangement give evidence of laborious research and very extensive scholarship. Special care seems to have been bestowed on the pronunciation and etymological derivation, and the 'root-words' which are given are most valuable in helping to a knowledge of primary significations. All through the book are evidences of elaborate and conscientious work, and any one who masters the varied contents of this Dictionary will not be far off the attainment of the complete art of 'writing the English language with propriety,' in the matter of orthography at any rate."—*Belfast Northern Whig.*

"This strikes us as likely to prove a useful and valuable work. . . . The number of scientific terms given is far beyond what we have noticed in previous works of this kind, and will in great measure render other special dictionaries superfluous. Great care seems also to have been exercised in giving the correct etymology and pronunciation of words. We trust the work may meet with the success it deserves."—*Graphic.*

"On the whole, we may characterise Mr Stormonth's as a really good and valuable Dictionary; and with the typical exceptions we have pointed out, we frankly allow his claim to have laboured earnestly and conscientiously in the production of it."—*Journal of Education.*

"I have examined Stormonth's Dictionary minutely, and again and again with satisfaction on points where other Dictionaries left me hopeless. It is an elaborate and splendid work, and with its great fulness, its grouping of words, and its meanings of phrases, should be the *vade mecum* of every student. It is a book I would like very much to see in the hands of all my advanced pupils."—*David Campbell, Esq., The Academy, Montrose.*

"I am happy to be able to express—and that in the strongest terms of commendation—my opinion of the merits of this Dictionary. Considering the extensive field which it covers, it seems to me a marvel of painstaking labour and general accuracy. With regard to the scientific and technical words so extensively introduced into it, I must say, that in this respect I know no Dictionary that so satisfactorily meets a real and widely felt want in our literature of reference. I have compared it with the large and costly works of Latham, Wedgwood, and others, and find that in the fulness of its details, and the clearness of its definitions, it holds its own even against them. The etymology has been treated throughout with much intelligence, the most distinguished authorities, and the most recent discoveries in philological science having been laid under careful contribution."—*Richard D. Graham, Esq., English Master, College for Daughters of Ministers of the Church of Scotland, and of Professors in the Scottish Universities.*

"For clearness of printing, neatness of arrangement, and amount of information, this Dictionary leaves nothing to be desired; while its correctness and condensed form giving all that is necessary with no redundance, will prove of great service to all who want a work of complete and easy reference, without having recourse to a Cyclopedia. In all cases where I have referred to the etymology, I have found it most satisfactory; once or twice after being unable to find a word in another Dictionary, I have met what I wanted in this one."—*John Wingfield, Esq., M.A.*

THE SCHOOL ETYMOLOGICAL DICTIONARY AND WORD-BOOK.

Combining the advantages of an ordinary Pronouncing School Dictionary and an Etymological Spelling-Book. By the Rev. **JAMES STORMONTH.** Fcap. 8vo, pp. 254, 2s.

"This is mainly an abridgment of Mr Stormonth's larger Etymological Dictionary, which has already been favourably criticised in 'The Schoolmaster.' The Dictionary, which contains every word in ordinary use, is followed up by a carefully prepared list of prefixes and postfixes, with illustrative examples, and a vocabulary of Latin, Greek, and other root-words, followed by derived English words. It will be obvious to every experienced teacher, that these lists may be made available in many ways for imparting a sound knowledge of the English language, and for helping unfortunate pupils over the terrible difficulties of our unsystematic and stubborn orthography. We think this volume will be a valuable addition to the pupil's store of books, and, if rightly used, will prove a safe and suggestive guide to a sound and thorough knowledge of his native tongue."—*The Schoolmaster.*

"For these reasons we always advocate the good old practice of teaching children English to a large extent by means of lists of spellings, all but the most elementary classes learning spellings with 'meanings.' Mr Stormonth, in this admirable word-book, has provided the means of carrying out our principle in the higher classes, and of correcting all the inexactness and want of completeness to which the English student of English is liable. His book is an etymological dictionary curtailed and condensed. . . . As a dictionary the book is very carefully compiled, and much labour has been expended on the task of economising words and space with as little actual loss to the student as possible. The pronunciation is indicated by a neat system of symbols, easily mastered at the outset, and indeed pretty nearly speaking for themselves."—*School Board Chronicle.*

"A concise handy-book of this kind was much wanted in schools, for most pocket-dictionaries are by no means reliable guides. Besides the word and its meaning, the pronunciation is given in each case, together with the kindred or root words in other languages. The work seems very complete."—*Educational Times.*

"The derivations are particularly good."—*Westminster Review.*

"This cheap and careful abridgment of Mr Stormonth's larger Dictionary, which has met with so cordial a welcome in all quarters, will be received as a boon by all interested in the education of the young. . . . We heartily endorse its claim to be 'a thoroughly practical school-book, and fitted for daily use by the pupil in and out of the school-room, in the preparation of the English lessons.'"—*Aberdeen Herald.*

"The work is admirably adapted for teaching the meanings of words, since after the meanings of the various postfixes have been learnt, the pupil will obtain excellent exercise in the formation of words derived from those given in the Dictionary."—*Mechanics' Magazine.*

NOW PUBLISHING.

ANCIENT CLASSICS
FOR
ENGLISH READERS

BY VARIOUS AUTHORS.

EDITED BY
REV. W. LUCAS COLLINS, M.A.
Author of 'Etoniana,' 'The Public Schools,' &c.

OPINIONS OF THE PRESS.

"We gladly avail ourselves of this opportunity to recommend the other volumes of this useful series, most of which are executed with discrimination and ability."—*Quarterly Review.*

"These Ancient Classics have, without an exception, a twofold value. They are rich in literary interest, and they are rich in social and historical interest. We not only have a faithful presentation of the stamp and quality of the literature which the master-minds of the classical world have bequeathed to the modern world, but we have a series of admirably vivid and graphic pictures of what life at Athens and Rome was. We are not merely taken back over a space of twenty centuries, and placed immediately under the shadow of the Acropolis, or in the very heart of the Forum, but we are at once brought behind the scenes of the old Roman and Athenian existence. As we see how the heroes of this 'new world which is the old' plotted, intrigued, and planned; how private ambition and political partisanship were dominant and active motives then as they are now; how the passions and the prejudices which reign supreme now reigned supreme then; above all, as we discover how completely many of what we may have been accustomed to consider our most essentially modern thoughts and sayings have been anticipated by the poets and orators, the philosophers and historians, who drank their inspiration by the banks of Ilissus or on the plains of Tiber, we are prompted to ask whether the advance of some twenty centuries has worked any great change in humanity, and whether, substituting the coat for the toga, the park for the Campus Martius, the Houses of Parliament for the Forum, Cicero might not have been a public man in London as well as an orator in Rome?"—*Morning Advertiser.*

"It is difficult to estimate too highly the value of such a series as this in giving 'English readers' an insight, exact as far as it goes, into those olden times which are so remote and yet to many of us so close. It is in no wise to be looked upon as a rival to the translations which have at no time been brought forth in greater abundance or in greater excellence than in our own day. On the contrary, we should hope that these little volumes would be in many cases but a kind of stepping-stone to the larger works, and would lead many who otherwise would have remained in ignorance of them to turn to the versions of Conington, Worsley, Derby, or Lytton. In any case a reader would come with far greater knowledge, and therefore with far greater enjoyment, to the complete translation, who had first had the ground broken for him by one of these volumes."—*Saturday Review, Jan.* 18.

Ancient Classics for English Readers.

LIST OF THE VOLUMES PUBLISHED.

1.—HOMER: THE ILIAD. By THE EDITOR.

2.—HOMER: THE ODYSSEY. By THE EDITOR.

3.—HERODOTUS. By GEORGE C. SWAYNE, M.A.

4.—THE COMMENTARIES OF CÆSAR. By ANTHONY TROLLOPE.

5.—VIRGIL. By THE EDITOR.

6.—HORACE. By THEODORE MARTIN.

7.—ÆSCHYLUS. By REGINALD S. COPLESTON, B.A.

8.—XENOPHON. By SIR ALEXANDER GRANT, Bart., Principal of the University of Edinburgh.

9.—CICERO. By THE EDITOR.

10.—SOPHOCLES. By CLIFTON W. COLLINS, M.A.

11.—PLINY'S LETTERS. By the Rev. ALFRED CHURCH, M.A., and the Rev. W. J. BRODRIBB, M.A.

12.—EURIPIDES. By W. B. DONNE.

13.—JUVENAL. By EDWARD WALFORD, M.A.

14.—ARISTOPHANES. By THE EDITOR.

15.—HESIOD AND THEOGNIS. By the Rev. J. DAVIS, M.A.

16.—PLAUTUS AND TERENCE. By THE EDITOR.

17.—TACITUS. By W. B. DONNE.

18.—LUCIAN. By THE EDITOR.

19.—PLATO. By CLIFTON W. COLLINS, M.A.

A Volume is published Quarterly, price 2s. 6d.